Primate Socioecology:
Development of a Conceptual Model for the Early Hominids

Daisy Kate Williamson

Dissertation submitted to the University of London for the degree of Doctor of Philosophy

University College London, Gower Street, London, WC1E 6BT

June 1997

ABSTRACT

This thesis is a cross-disciplinary project, drawing on the techniques of behavioural ecology to reconstruct aspects of the socioecology of the early hominids. The modelling approach advocated in this project is an attempt to move towards the conceptual modelling approach forwarded by Tooby & DeVore (1986), moving away from referential and phylogenetic primate models to reconstruct hominid social behaviour. The project contributes to one current aim in palaeoanthropology; to develop a theoretical framework with which to reconstruct the behaviour of extinct taxa. The raw data for these models come from comparative analyses of behavioural ecology of extant primates.

The fundamental basis of systems models of socioecology, is that the relationship between the environment and behaviour is characterised. The choice of environmental parameters has proved to be crucial, therefore I have characterised the key environmental variables that affect animals both directly (e.g. thermoregulatory stress), and indirectly (e.g. via habitat productivity). The quantitative relationships found in this chapter will serve as useful constants for further models.

I first present a re-analysis of the systems models of baboons, refining previous models by R. Dunbar. The statistical techniques underlying these linear program models was further supported by the stability of the models when new data were included. Long-term climate data that were accurately sited were found to produce the most predictive equations. The results of the reanalysis of the baboon models gave support to their extension to another taxa.

I then extend the range of the time-budget based models to the chimpanzees. The initial focus on chimpanzees is not solely because they are phylogenetic analogues. The emphasis of the models is that they are habitat specific. Relationships between behaviour and environment are used to develop functional equations to explore an animals flexibility of response to varying environmental conditions. Predictions could be made about; maximum ecologically tolerable group size, territory size, diet and extent of geographic range. The geographic distribution of chimpanzees predicted by the model was found to match very closely the current distribution.

The models of chimpanzee, baboon and gelada socioecology were then compared. Dietary differences between the taxa accounted for their ecological niche separation.

The models of extant primate systems models developed in this thesis provide a firm foundation for extending the models to extinct taxa. Preliminary models are presented, extending these analyses to the extinct australopithecines to forward the development of a conceptual model for the early hominids.

ACKNOWLEDGEMENTS

I would like to thank both my supervisors, Leslie Aiello and Robin Dunbar for their support during the research and completion of this thesis. Upon Robin Dunbar's move to the Department of Psychology, University of Liverpool in October 1994 I am most grateful to the University of Liverpool for giving me 'honorary research assistant', status, so that I could continue my research in Liverpool. I would like to thank the Department of Psychology, University of Liverpool, for the use of resources and research facilities during my year there. This research was funded by an NERC studentship and University College London postgraduate research fund.

In Liverpool I would like to thank the following for their hospitality and support on my move to Liverpool: Louise Barrett, Laura Harste, Tracey Joffe, Nicola Koyama, Catherine Kenyatta, Sam and Chris Lowen and Rosalia Pastor-Nieto. Finally to Barony Baty, for making me welcome in her home on my frequent visits to Liverpool, and for her support during the completion of this thesis.

In London, I would like to thank the following for their help and support over the past three and a half years; Leslie Aiello, Clare Holden, Cathy Key, Ruth Mace, Daniel Nettle and Rebecca Sear. To Iain and Jo Smith, for allowing me to house sit on several occasions when moving between London and Liverpool.

Thankyou to the Government of South Africa for granting me a research permit to enter South Africa, and to Jeff McKee at the department of Anatomy, The University of Witwatersrand, for granting us permission to conduct research at Makapansgat.

Finally, my special thanks go to my family, Nichola and Rupert Williamson, for their emotional and financial support over the past few years. Finally I would like to give my extra special thanks to Charlie Underwood for his support and encouragement.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Chapter 1. Introduction

Chapter 2. Ecological correlations

CHAPTER 1. INTRODUCTION

1. INTRODUCTION

> "What was it like to be a hominid foraging on the African savannah two million years ago? The latter approach requires a kind of holistic natural history wherein various lines of paleo-evidence, modern analogues and actualistic experience are brought together within a sequence of auxiliary conceptual frameworks to create models of early hominid life-ways" (Peters & Blumenschine 1995)

One of the principal aims in current palaeoanthropology is to understand hominid behaviour. Palaeoanthropology draws on a number of sub-disciplines in order to develop meaningful accounts of hominid evolution (Gifford 1981). Uniformitarianism is the central principle that underpins research into past events and processes (reviewed in Gifford-Gonzalez 1991). Processes that shape an organism or its behaviour are assumed to be uniform through time. Therefore it should be possible to extrapolate through time if the processes that underlie it are sufficiently quantified and understood. There are broadly two categories of studies in palaeoanthropology; diachronic (studies concerned with evolutionary transformations and culture change) and synchronic (including those studies which attempt to reconstruct life in past-history). This thesis is concerned with the latter, developing models, within a sound theoretical framework, with which to reconstruct the behavioural ecology of the early hominids. However, as yet there are no established methods for analysing the behavioural ecology of individuals of extinct species. Behavioural ecology emphasises the function, or survival value of a behaviour (Krebs & Davies 1984), behaviour being influenced and responding to the constraints and requirements of the animals ecological context. Any attempt to reconstruct the behavioural ecology of extinct species must therefore be ecologically grounded in the extinct species' specific palaeoenvironmental context (Oliver *et al.* 1994). The behavioural ecology of extant animals considers behaviour over relatively short time-scales; 'short-term slices' through evolutionary time (Gowlett 1996). The patterns of behaviour observed today are the product of evolutionary processes acting over greater periods of time. Evolutionary ecology, as an integrated science, focuses on optimal traits, to provide a mechanistic understanding of ecological patterns. The behavioural

ecological perspective to reconstructing the behaviour of extinct hominids starts from the premise, that the same ecological principles and processes that underlie behaviour today are likely to have operated in the past.

In this chapter I shall firstly briefly review the historical development of models to investigate extinct hominid behaviour, to place the modelling framework advocated in this thesis in context (1.1). I then outline in detail, with examples the development of recent models based on evolutionary ecology (1.2-1.3). In section 1.4 I outline sources of data available with which to construct the models presented in this thesis, and conclude with an outline of the thesis (1.5).

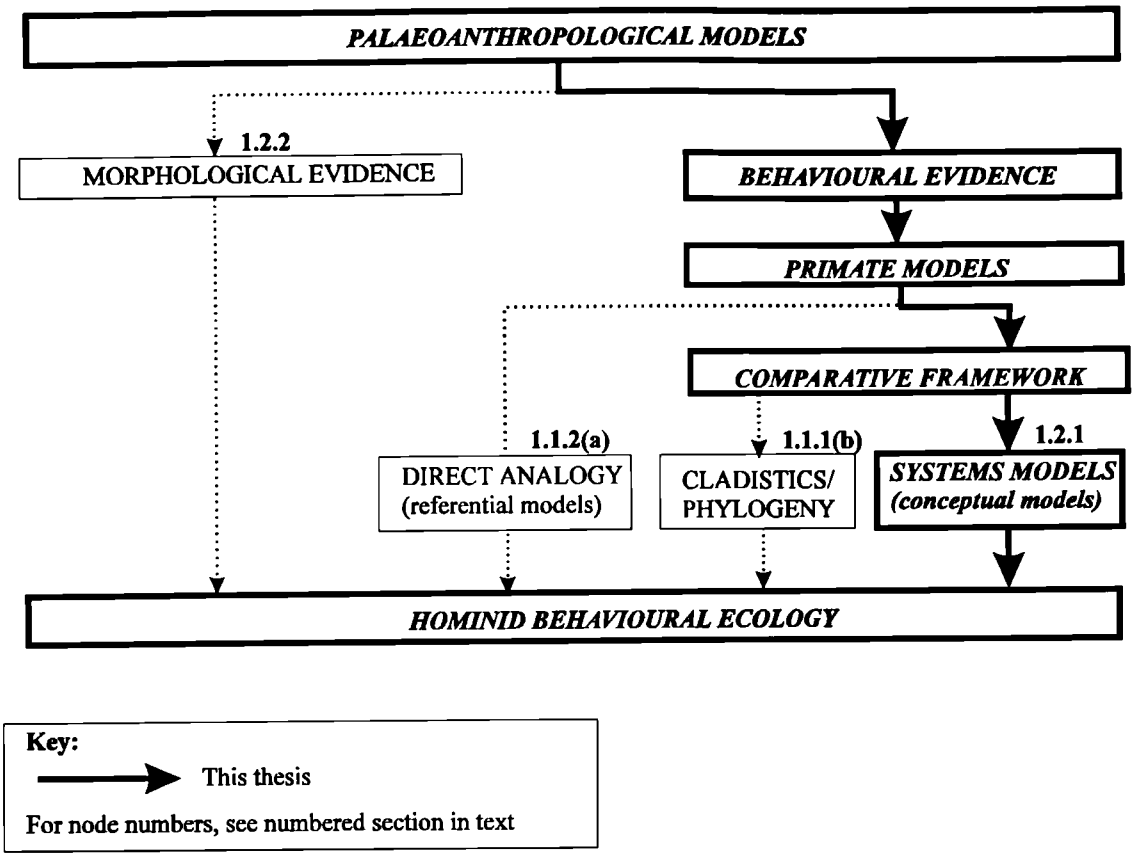
1.1 APPROACHES TO MODELLING HOMINID BEHAVIOURAL ECOLOGY

1.1.1. Historical perspective

Models on the evolution of hominid behaviour may be classified broadly into two groups Primate derived models, and those reconstructing behaviour from morphology. Morphological derived models have assessed, for example; ecological niche based on general morphology (e.g. Szalay & Delson 1979) and determination of specific traits, by extrapolation from allometric scaling relationships for modern primates (e.g. Kay & Simons 1980; Kay & Covert 1984).

The physical, archaeological remains are viewed by some to be the central elements in reconstructing hominid behavioural ecology (Blumenschine *et al.* 1994). However, not all aspects of hominid social behaviour are accessible via the archaeological evidence, therefore further techniques are needed to investigate such issues as group size, mating system, home-range etc. One approach is to use comparative data from extant primates. Primate derived models may be further subdivided into categories (see fig. 1).

Figure 1.1. Schematic diagram of the categories of primate derived models with which to reconstruct aspects of hominid behaviour.



In the following sections I shall review the advantages and disadvantages of the different primate models, ultimately focusing on the systems models that are the focus of this thesis.

1.1.2. Comparative approaches

First, a distinction should be made between two broad classes of models; top-down and bottom-up models (Dunbar 1989). Top-down and bottom-up models are distinguished by both the data used to construct them, and the inferences that can be made from them. Top-down models describe biological systems; in this way inferences can be made about other species (in this case an extinct species) by projecting from more general relationships that we see in living forms. By contrast, bottom-up models construct the biological system from first principles, identifying the selection pressures that might have

given rise to the phenomenon as we see it now. This dichotomous classification can be applied to existing approaches in modelling hominid socioecology. Neither approach is mutually exclusive, and as I shall show in this thesis, may indeed be complementary.

Tooby & DeVore (1987) reviewed and categorised models of hominid behaviour presented in Kinzey (1987). The models could be grouped into referential and conceptual models. Referential models use some existing behaviour or species (e.g. hunter gathering or a primate species) as a referent for another phenomenon that is inaccessible to study (e.g. hominid behavioural evolution). Conceptual models are "based on theories: sets of concepts or variables that are defined, and whose relationships are analytically specified" (Tooby & deVore 1987: 185). Evolutionary theory is the unifying concept with which conceptual models are built.

In the following section I critically review existing examples of referential and conceptual models.

i. Referential models

Referential models are often used in physical anthropology, however the hominid skeletal fossil record is limited. The sample size of critical skeletal elements is insufficient for many detailed comparative studies, limiting the implementation of this approach. Further to this, social behaviour leaves no physical evidence in the early non-tool making hominids, therefore many living species have been proposed as referents for early hominid behaviour.

Referential models attempt to identify similarities and differences in the behaviour of humans and extant primates, and attribute the similarities to conserved patterns of behaviour retained by humans and the primate used as the referent, from their common ancestor. Many living species have been proposed as referents for the early hominids: common chimpanzees (e.g. chimpanzees (McGrew 1981; Prost 1985; Tanner 1981; 1987; Susman 1987); bonobos (e.g. Zihlman *et al.* 1978); baboons (e.g. Jolly 1970; Dunbar 1976; reviewed in Strum & Mitchell 1987), living hunter-gathers (reviewed in Teleki 1981); social carnivores (e.g. Schaller & Lowther 1969), and more general cross-

species comparisons (Reynolds 1976). The primate data in referential models have been considered to provide a baseline, which can then be applied by analogy to extinct species (Strum & Mitchell 1987). Baboons and chimpanzees are commonly chosen as referents. Chimpanzees are often selected as homologues (similarity due to common descent), and baboons as analogical models (similarity due to common adaptation). However, unrelated species have been chosen as referents, for example howler monkeys (Crockett 1987). The value of Crockett's model was to emphasise the wider principles of behavioural ecology to particular categories of behaviour. For example, that a single species may occupy a wide range of habitats even though it has a single 'feeding niche', and that seasonal differences in behaviour may be greater than habitat differences (Crockett 1987).

Referential models may be criticised for several reasons. Primarily, the referential method emphasises similarities at the expense of differences. For this reason it is impossible to ask questions about features unique to human evolution (Foley 1987; Potts 1987; Cartmill 1990). Once a referent species has been chosen, as an analogue or homologue of the species in question, characteristics must be chosen to compare with the extinct species. The criteria for selecting characters for comparison have been criticised. Referential models cannot reveal along how many dimensions the model resembles the unobservable referent (i.e. the extinct hominid ancestor). There is a danger too that referential models become static reconstructions. By selecting particular aspects of species for comparison, variance in those behaviours and the factors that influence that variance are ignored. Patterns of human evolution must be tested against general evolutionary and ecological principles, not reconstructed from specific assumptions about the nature of human species (Foley 1987). Analogical models, from an evolutionary point of view, are *post-hoc* (Lee 1989). They depend on unstated assumptions about the basis of the similiarity between the referent and focus species, and also are highly selective about the evidence used. By contrast models drawing on evolutionary principles are preferred here (see chapter 3), since they return to evolutionary first principles without the use of hindsight.

Not only has the underlying theory for the construction of referential models been criticised, but also their ultimate aim (Moore 1996). An example of this is the 'pygmy chimpanzee' model of Zihlman (1978) (see Moore 1996 for a review).

Despite these criticisms, some authors still advocate that referential models are useful (Potts 1987; McGrew 1992; Moore 1996). Moore (1996) in particular uses a referential model that is not based on a single typological modern species (chimpanzee), but the set of differences between populations of the highly variable referent chimpanzee species. Moore (1996) does not select the 'typical' chimpanzee for comparison, but takes into account variation in behaviour to select the relevant characteristics for analogy. Intraspecific variability in the referent species is used to model diachronic change in the hominid lineage (Susman 1987), thereby emphasising process, not stasis (Potts 1987). In archaeological terms, this latter approach is relational, as opposed to a formal analogy (Gifford-Gonzalez 1991). Relational analogies take into account the context and variability of the referent to select the relevant criteria for comparison. However, with no underlying conceptual theory with which to base the comparison, it is unclear along what dimensions the model species resembles the unobservable referent species (Tooby & DeVore 1987). By focusing on the extant apes as referents, these models focus on the period of our evolutionary history when the differences between extinct hominids and extant apes is assumed to be minimal.

ii. The cladistic method (phylogenetic referential models)

Socioecological models may require that we take phylogeny into account. Phylogenetic referential models, using a wide range of criteria (see Andrews & Aiello 1984; Ghiglieri 1987; Wrangham 1987; Foley 1989; Foley & Lee 1989; Rodseth *et al.* 1991; Cameron 1993; Begun 1994; DiFiore & Rendall 1994; Maryanski 1996) have been conducted to identify suites of characters shared by the common ancestor of humans, chimpanzees (*Pan troglodytes*), bonobos (*Pan pansicus*) and gorillas (*Gorilla gorilla*). These models take the view that the behaviour of humans and apes parsimoniously explains the behaviour of their last common ancestor (LCA). They map behaviours onto resolved

phylogenys, to reconstruct behaviour at ancestral nodes. The cladistic method avoids the assumption of referential models, that an extinct species could not have been uniquely different from a modern analogue. However, cladistic conclusions are restricted to those traits that are shared by all the modern taxa used in the analyses. Therefore the cladistic method is incapable of identifying differences between hominids and apes.

Ghiglieri (1987) further linked phylogeny with the behaviour of the LCA, by linking principles from behavioural ecology and sexual selection theory. This approach was an advance towards a more integrated approach. It combined a behavioural ecological approach with the phylogenetic one, however the analysis was restricted to a verbal argument.

A number of studies of this sort (e.g. Baer & McEachron 1982; Picq 1993; Isbell & Young 1996; Rose & Marshall 1996) are presented in a behavioural ecological framework, referring to the analysis as a model. These studies present a comparative discussion in the light of knowledge of the behavioural ecology of extant species. This differs from the definition of a model in behavioural ecology (*sensu* Moore 1996, and see section 1.3).

The cladistic method may be used to investigate the evolution of social behaviour in the hominoids, characterising 'phylogenetically inherited socioecology' (Foley 1989; Foley & Lee 1989). This approach relies on distinguishing derived (plesiomorphic) characters from ancestral (apomorphic) characters. However this distinction is far from clear when considering social traits. Assigning social-systems to a cladogram ignores the fact that social systems are very much habitat specific, given phylogenetic constraints (Dunbar 1988). Nevertheless, an important contribution of this approach was to identify phylogenetic constraints on behaviour, the mapping of evolutionary pathways, and identifying the rules that govern the development of those pathways (Foley & Lee 1989).

The framework of behavioural ecology is the view that behavioural strategies as individual responses to environmental variation. Primates do not show species typical behaviour (Strier 1994), for example, recent data has shown inconsistencies between populations of the same species, in the sex which emigrates from the social group (e.g.

Moore 1992). Without characterising those factors which account for variation in extant behavioural strategies, we are not in a position to extrapolate to the extinct hominids. Phylogenetic reconstructions rely on a model of evolution or an assumption about how changes occur. This is unlike referential models, which are based on a single-species. This can be seen as an advantage (Rendall & DiFiore 1995). Additionally, phylogenetic methods need not consider all behaviours as a 'suite'. They can consider only those features of the referent species thought to be relevant to the extinct hominids. Additionally, phylogenetic models can be useful in guiding our selection of referent species. For example DiFiore & Rendall (1994) found that the Old World monkeys were not the most appropriate models for the early hominids, being too derived with respect to other primates.

iii. Conceptual models

Tooby and DeVore (1987) advocate that we need a more sophisticated modelling approach that is capable of reproducing the fine-tuned responses of animals to the many different variables that influence their behaviour.

> "To progress, we must discard prime-mover and single-species primate models of human evolution and instead recognise that evolutionary biology provides the conceptual model that will organise our understanding of hominids" (Tooby & DeVore 1987).

Conceptual models are not real phenomena, but theories or sets of concepts. These theories are carefully defined and the interrelationships specified. Tooby & DeVore (1987) proposed the term 'strategic modelling' to describe the construction of these conceptual models. Referential models of hominid behaviour assume that the referent species behaves in a species typical way. However, primates are characteristically variable in their demographic, social and ecological patterns across a range of habitats (e.g. Melnick & Pearl 1987; Smuts *et al.* 1987; Dunbar 1988). There is no species-typical social system, the longer a species is studied, and over a wider range of habitats, more variation is found in a species social system. Therefore social systems may be

artificial constructs, which may hinder our understanding of social behaviour (Rowell 1994).

The conceptual approach aims to develop a set of inferential procedures that are deduced from evolutionary theory. The models may then be refined with empirically validated evolutionary biology, phylogenetically honed by primate studies and fitted with specific archaeological and palaeontological evidence. The models must have a firm grounding in evolutionary biology and be linked the available evidence on the extinct species. Lee (1989) devised a hierarchy of inferences with which to infer the behavioural ecology of extinct hominids. These inferences emphasise the function of a behaviour and its ecological correlates, before building on these to make higher order inferences.

Table 1.1. The different levels of inference that can be used to predict hominid behaviour.

Primary inferences (from fossils)	1. environments (food type, patchiness, competitors / predators) 2. morphology (body size, brain size, dimorphism, diet)
Secondary inferences	1. Life history variables 2. Distribution of males and females 3. Nutritional and foraging requirements
Tertiary inferences	1. Social dynamics 2. Reproductive / parental strategies 3. Demographic variables

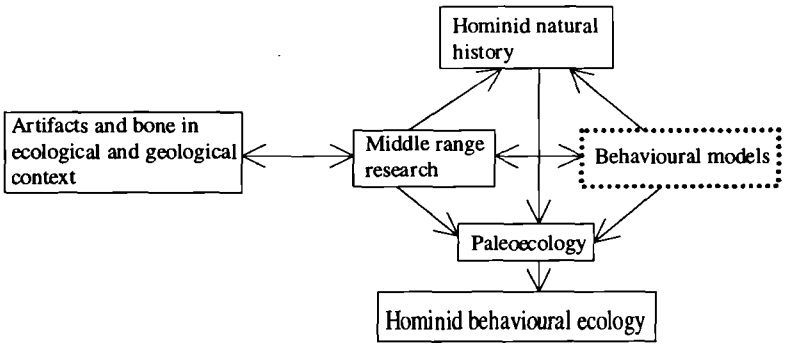
The controlling theory for accessing pathways to the past is evolutionary theory. Evolutionary ecology is then employed to identify the adaptive problems and predict solutions, based on general biological principles. It is through this chain of inferences that we hope to explore further the behavioural ecology of the early hominids (see Foley 1987, fig 4.5: 88).

1.1.3. The archaeological perspective of conceptual modelling

Inferential procedures for reconstructing the behaviour of extinct species have often been viewed in archaeological terms. A review of strategies needed by palaeoanthropologists to gain greater inferential confidence when interpreting the behavioural systems and

regional ecosystems of extinct hominids was outlined by Gifford-Gonzalez (1991). The term 'middle-range theory' (Binford 1977, 1981) is used by archaeologists as analogous to conceptual modelling when reconstructing past behaviours. Both theories bring together aspects of the past to processes that work in the present. Like conceptual modelling, the emphasis is on process, and dynamics of interactions can be investigated. Research using the principles of 'middle range theory' (middle range research) traces the link between modern behavioural processes and the traces it would have left in the archaeological, geological and palaeontological records. Middle range researchers have been successful in documenting specific hominid activities (e.g. stone tool manufacturing, diet, locomotion). A schematic framework for conceptualising the study of hominid behavioural ecology (see fig. 1.2) has been reviewed by Blumenschine *et al.* (1994). This framework integrates sources of evidence from several related disciplines; hominid and archaeological remains, palaeoenvironmental evidence, and behavioural models of extant primates.

Figure 1.2. A schematic framework for conceptualising the study of hominid behavioural ecology. The vertical represents the contribution of extinct hominids, the horizontal axis the taphonomic and naturalistic studies of modern processes and organisms applied to hominid fossils, archaeological remains and the palaeoenvironmental evidence. (Adapted from Blumenschine *et al.* 1994; fig.1: 198).



Before applying behavioural ecological models to fossils, the implications must first be interpreted into the "language" of the fossil record, through middle range research (Blumenschine *et al.* 1994). In this way the fossils are taken as the final arbiter of a models' success. The resultant model must therefore not be inconsistent with the fossil

record. Ultimately, the evidence available will limit the particular applications of behavioural ecological models.

Models based on evolutionary theory are likely to be the most useful in identifying behavioural and ecological parameters (Steele 1996). Behavioural ecological models can identify particular behavioural strategies, given specific environmental parameters. However, given the flexibility of behaviour in response to environmental variables, these models have the potential to explore a range of behaviours, 'different ways of being a hominid' (Foley 1987).

The behavioural ecological perspective in reconstructing early hominid behaviour is relatively new. The earlier work on Plio-Pleistocene sites focused, primarily on scavenging opportunities open to the early hominids (e.g. Blumenschine 1986, 1987, 1991; Bunn & Kroll 1986; Potts 1987; Marean 1989; Bunn & Ezzo 1993). Latterly there has been a move towards landscape archaeology, reconstructing palaeoenvironments (e.g. Potts 1989; Blumenschine & Masao 1991; Sept 1992; Bunn 1994; Stern 1993, 1994). These two approaches have facilitated the comparison of resource availability between sites and the consequences for early hominid socioecology (Potts 1994).

'General theory' applies general ecological principles, relating aspects of the environment to behavioural responses in a wide range of species in different habitats (Blumenschine *et al.* 1994). There has been a debate amongst archaeologists as to whether we shall ever achieve a fully integrated approach between the fossil evidence and behavioural models (see Gowlett 1996). However, there need not be a debate, since the fossils lend themselves to different fields of study (locomotion, diet etc.), to ecological studies, which place this behaviour in context.

1.2. MODELLING HOMINID BEHAVIOURAL ECOLOGY: Extrapolating behavioural ecology beyond the present time frame.

There are well established interactions between ecological and behavioural variables (e.g. Rubenstein & Wrangham 1986; Smuts *et al.* 1987). Habitat, resource-base, diet, body

size, life history parameters and social relationships are all tightly integrated. Animals show great flexibility in their capacity to respond to environmental change (e.g. Lee 1991). The characterisation of the relationship between behavioural and ecological variables allows extrapolation to past environments. No extant primate is strictly analogous to any early hominid. This thesis proposes a more comparative approach. The early hominids were subject to the same types of selection pressures, (e.g. predation risk and resource competition), as living primates (e.g. Dunbar 1996) thus the response of the early hominids would have been consistent with trends found today (Rose & Marshall 1996). The data on extant primates required for comparative socio-ecology must have been collected over significant time-periods, particularly in large, long-lived primates. Long-term data is particularly important when examining behavioural responses to environmental change over time. Most studies are short, averaging less than two years (Dobson & Lyles 1989), however there have been significant numbers of long-term studies for comparison (e.g. Goodall 1986; Nishida 1990). Therefore there is sufficient data to extrapolate from current behaviour to testing hypotheses on the behavioural ecology of extinct species. Indeed, there is now sufficient comparative data to make inter-continental comparisons between extant taxa (Fleagle & Reed 1996).

1.2.1. Systems models

Systems models quantitatively examine the relationship between the components of a system, in this case a social system. Causal relationships between components are examined, for instance between ecological and behavioural variables. The systems model approach contrasts with the referential models, in that it is population specific, rather than species specific. Species are considered in systems models as those individuals that happen to share a set of ecologically relevant characteristics (e.g. body size) and a particular bauplan with respect to dietary and reproductive specialisations (Dunbar 1992*e*).

Dunbar (1992*a*, *b*) developed such systems models, using comparative data available on two cercopithecine primates; *Papio* baboons and gelada baboons

(*Theropithecus gelada*). Variations in life-history and behavioural parameters were compared in relation to key environmental variables (e.g. Dunbar & Sharman 1983; Iwamoto & Dunbar 1983). Physiological constraints on of the species guided the selection of key environmental variables (Kleiber 1961; Tokura *et al.* 1975; Taylor *et al.* 1980; 1982). Inter-population variation in body weight in *Papio* baboons demonstrated the multivariate approach for inferring causal relationships between environmental, behavioural and morphological variables. Male and female body weights were related to primary productivity, indexed by mean annual rainfall (Dunbar 1990).

This multivariate approach was used to determine group size from time-budgets of extant species, and was then extrapolated to extinct taxa (Dunbar 1992 *a, b, e,* 1993*a,* 1994, reviewed in 1996; but see Bronikowski & Altmann 1996). The way an animal allocates time to essential activities is an optimisation problem, where carrying out one activity results in lost opportunities to carry out another. Therefore time has to be allocated to maximise benefit in the available active day (McFarland 1974; Caraco 1979*a,b*, McFarland & Houston 1981). By developing functional equations, relating environmental and physiological constraints, a habitat specific optimum group size could be determined. A set of equations relating environmental and ecological variables were computed, representing the costs and benefits of group living. Group size is at the intersection of a set of benefit and cost equations, a 'state-space' of realisable group sizes is created. The state-space in optimality literature in animal behaviour, describes a hypothetical space an animal occupies, when optimising a criterion (e.g. group size) which is dependent on the animals state (e.g. time constraint). Animals will live in the largest group a habitat will allow, the 'maximum ecologically tolerable group size' (see chapter 3). Predictions can then be made about geographical distribution. Populations are prevented from surviving in those habitats where the constraints on their time-budgets are too great. Further questions can then be asked whether a grade shift in dietary strategy, cognitive capacity or body size (which has consequences for life-history parameters) would allow an animal to survive more effectively under the same ecological conditions. This approach has successfully been extended to extinct Papionines and

Theropithecines (Dunbar 1992*a*, 1993*a*; Lee & Foley 1993). If we can quantify the functional relationships between environmental and behavioural variables in extant primates, we are in a stronger position to understand the evolutionary history of extinct lineages, and the selective pressures that lead to their extinction (Foley 1991, 1994; Lee & Foley 1993). The location of hominid fossil remains, indicates that a hominid could survive in that particular paleo-habitat. By exploring in more detail the ecological constraints on an animals ability to colonise habitats, we may be able investigate further the selection pressures that may have driven changes in dietary strategy, body size etc.

Preliminary predictions show that *Theropithecus oswaldii* went extinct in the Pleistocene because they were unable to cope with a deterioration in habitat conditions following a dramatic climate change (Dunbar 1993*a*). Extrapolating functional equations derived from extant primates to extinct taxa requires a range of specific data. These data include key variables such as; body weight, basic palaeoenvironmental data and that the ecological context of the extant model species is comparable to that of the extinct species. Models can show whether a particular extinct species could survive in a specific habitat. If the model showed it could not survive in that habitat, the shifts in strategy that would be needed in order to survive there could be simulated. The emphasis of these models is they are habitat and taxon specific. Key to this type of analysis is the availability of sufficiently detailed paleoclimatic data, to extend the approach from extant species. The palaeoenvironmental data should be specific to time and place if we are to say how a given taxon with its own particular dietary and reproductive strategies is likely to have responded.

The advantage of the systems model approach is that it takes into account inter-population variance in extant species' behaviour. Comparative analyses reveal in more detail the constraints acting on behaviour, which data on a 'typical' population would not provide. Understanding how a biological system is structured, through systems models points to testable predictions. Evolutionary theory predicts that animals will act to maximise their genetic fitness. By defining the multi-dimensional space an animal

occupies, we can then locate alternative strategies on the basis that animals will minimise costs and maximise benefits. This cost-benefit approach is one theoretical framework with which to move towards the 'conceptual' modelling approach advocated by Tooby & deVore (1987).

1.2.2. Allometric scaling models

There are established relationships between body size and behaviour, which can lead to many higher order inferences. For example, body size variation in mammals is related to life-history variables (e.g. neonatal brain size, neonatal body weight, gestation length, weaning age, age at maturity, age at first breeding, inter-birth interval, and life span; Harvey & Clutton-Brock 1985). Body size is also related to the metabolic cost of locomotion, population density, home-range size, social organisation (sexual dimorphism), diet, cognitive skills etc. (Blumemberg 1981, 1983, 1984, 1985; Calder 1984; Damuth 1981; Damuth & MacFadden 1990; Foley 1992; Martin 1983; Aiello & Dunbar 1993; Dunbar 1992*a*). The behavioural ecological implications of early hominid body size are reviewed in McHenry (1994). Reproductive and social factors, such as greater longevity, longer gestation and inter-birth-intervals, lower birth rate and increased sociality and brain size may all be primary consequences of increase in body weight (Foley 1987). The likely causes of increase in body size are ecological factors, specifically those aspects of the environment related to energetics and availability and access to resources. With information on group size and inter-birth intervals the mating system of an extinct species may be determined (Dunbar 1988).

Home-range size in mammals, for example may be determined by a simple allometric relationship between group mass and home range size (Grant *et al.* 1992). Previous studies on home-range size in early hominids have looked at lithic tool transport distances (e.g. Foley 1987; Steele 1996). Raw material transport is taken as evidence of the minimum diameters of home-ranges. Home range size scales to group mass (the total biomass of a social group) in mammals (Grant *et al.* 1992). The data required for this approach are; group size and species weight. Estimates of these parameters for the

early hominids are available (group size: Aiello & Dunbar 1993; species weight: e.g. McHenry 1994). With an estimate of home-range size, related issues such as territoriality can be predicted (Mitani & Rodman 1979; but see Lowen & Dunbar 1994).

1.2.3. Environmental models

Behavioural models may be constructed to take account of habitat variation. Fluctuations in habitats and resources may have driven natural selection. Heterogeneity of environments are important, therefore this should be taken into account in palaeoenvironmental reconstructions. Paleoenvironments vary over time in climate and related landscape features (e.g. Feibel *et al.* 1991; Rayner *et al.* 1993). When constructing models of early hominid foraging (Potts 1994), no one behavioural reconstruction will encompass that variability. Site-specificity is key in such reconstructions (Sikes 1994). Stochasticity is important, since natural selection over time would have acted in response to habitat and resource variability over time. Behavioural responses should therefore be modeled in relation to habitat and resource variability (see Mangel & Clarke 1986).

With habitat variability in mind, environmental seasonality has been investigated with respect to seasonally available resources (Foley 1993; Stewart 1994).

Foley (1993), for example examined the consequences of seasonality, for group size, dietary specialisation and geographical radiations among the extinct hominids.

1.2.4. Physiological constraint models

A recent development of 'top-down' models of hominid behaviour has been to extrapolate physiological constraints of extant species to extinct species to make more detailed predictions about such issues as; dietary evolution (Aiello & Wheeler 1996); bipedalism, foraging day length and home-range area, (Wheeler 1984, 1991*a,b*, 1992*a,b*, 1994*a,b*, 1996; but see Porter 1993; Chaplin *et al.* 1994; Amaral 1996). In addition physiological constraints have been used to model possible habitats for the early hominids (Ruff 1991; Wheeler 1993). Upon comparing *Homo* and Australopithecine

physiques, it has been shown that the *Homo* physique is advantageous for thermoregulation in open habitats. *H. erectus* would most probably have been limited to relatively dry/open environments, while the Australopithecines could have inhabited either open/dry or closed/wet environments (Ruff 1991).

These 'second generation' conceptual models (*sensu* Dunbar 1989), based on physiological principles, allow us to gain further insight into the behaviour of the early hominids

1.3. MODELS IN BEHAVIOURAL ECOLOGY

There has been debate as to the definition of an ecological model (see above). This is reviewed in detail by Moore (1996). Rendall & DiFiore (1995) hold the view that models reconstructing the behavioural ecology of extinct species are inherently unfalsifiable, based on the lack of independent evidence with which to test the models. However, properly conceived, constructed and validated models provide perhaps the only opportunity to explore hypotheses in the field of 'extinct behavioural ecology'.

The aims of models in behavioural ecology, are to better understand the constraints acting on individuals, and functional significance of behaviour. Functional relationships in a model should be derived from a large enough sample size, and the derived relationships make sense within a theoretical framework. A successful model is characterised by its ability to organise and interpret existing data, and still be flexible enough to incorporate new data as it arises. As inferences are made, additional indirect evidence can be focused on the model, expanding the possible inferences that can be made from the model. Models simplify underlying processes (see Lendrem 1986), and also make explicit the primary influences on those processes, integrating data into sound theoretical frameworks. Models can function as descriptive tools, when they are assembled from component parts. These bottom-up models function to predict the future behaviour of the system, and reveal further the workings of the system. The precision of quantitative models reveals in greater detail relationships between variables.

A conceptual model has elements that are well-defined, and easily implemented. The relationships between variables are sharply constrained, and the assumptions upon which the model was constructed are validated. If not validated, the assumptions of the model should be at least both realistic and clearly stated. The model should make potentially falsifiable predictions, and the same few elements should economically explain a large range of phenomena.

The model itself should be self consistent, predicting the data on which it is based. A more powerful alternative is to search for consequences of the model that can be tested. In an integrated system, changing the value of one variable may upset the system. By changing an input value in this way, the robustness, or sensitivity of a model can be investigated . This helps to test whether the theoretical basis of the model is correct and that the assumptions on which it was based were true (see Belovsky 1994; and chapter 3). Each variable is altered in turn to assess its effect on fitness (reproductive success), (e.g. Terborgh 1983; Dunbar 1984*a*). Any model must make clear the distinction between ultimate causation (phylogenetic constraints) and proximate causation (local environmental constraints). Models of socioecology may represent the only opportunity to explore in detail the complexity of social strategies in an evolutionary framework.

1.4. AIMS

The aim of this thesis is to develop a series of models with which to reconstruct aspects of the behavioural ecology of the early hominids. These models will focus on the 'conceptual' approach, built up from the principles of evolutionary ecology. Complementary models will also be developed. Contrasting systems models from the 'top-down' modelling perspective, and complementary 'bottom-up' models, rebuilding from biological first principles. Whilst different extant primate species will serve as referents in the systems models, the extinct taxa of focus in this thesis are the Australopithecines.

1.5. THESIS OUTLINE

The fundamental basis of systems models of socioecology, is that the relationship between the environment and behaviour is characterised. The choice of environmental parameters has proved to be crucial (e.g. Bronikowski & Webb 1996). The analyses presented in chapter 2, seek to characterise in more detail the key environmental variables that affect the animal directly (e.g. thermoregulatory stress) and indirectly (e.g. habitat productivity). These equations are then employed in chapters 3 and 4. Chapter 3 presents re-analyses of systems models of baboons, refining previous models by Dunbar (op. cit). Chapter 4 extends the range of the time-budget based models to chimpanzees as a further referent species for the extinct hominids. Chapter 5 compares the socioecological models developed on baboons, gelada and chimpanzees and extends the models developped on extant primate taxa to the extinct early hominids. In the discussion, suggestions are made for the further development and extensions of the models presented in this thesis.

CHAPTER 2. ECOLOGICAL CORRELATIONS

CHAPTER 2. ECOLOGICAL CORRELATIONS

2.1 INTRODUCTION

The basis of behavioural ecology is to understand the relationships between behaviour and environmental constraints. In this chapter I carefully define environmental variables to be used in chapters 3 and 4. A limiting factor in the investigation of the effect of climate as a limiting factor, has been the availability of sufficiently detailed climate data. In particular, long-term climate data from specific field sites is rare, reflected by the relatively high frequency of short-term field studies (Dobson & Lyles 1989). The ultimate aim of climatic variables is to characterise habitats in terms of limiting factors. These effects may be direct (e.g. thermoregulatory stress in high temperatures) or indirect (e.g. food availability indexed by rainfall). In this chapter I review and test a range of indices of habitat productivity. The minimum number of variables needed to characterise a habitat are determined, and these variables are then used as inputs in models of baboon socioecology (chapter 3) and chimpanzee socioecology (chapter 4).

2.2. RAINFALL INDICES OF HABITAT TYPE

The main climatological criteria influencing plant and animal life are water availability and temperature. Many climatic parameters control vegetation locally. However, heat and water relations are the most important habitat and environmental factors when classifying the geo-biosphere (Walter 1979; le Houérou & Popov 1981). In a systematic world-wide analysis of vegetation and environment, Box (1981) found plant form and vegetative structure to be primarily determined by temperature and water balance. Soil type, topography and the biotic components of an environment are important in determining plant growth in addition to climate (Walter 1979; Daubenmire 1978; Whittaker 1965). Shultz & McGee (1978) reviewed vegetation patterns in southern Africa. They found that the climatic variables determining the location and distribution of vegetation associations were seasonal fluctuations in the duration and intensity of precipitation, temperature and incoming solar radiation. These climatic variables

essentially reduce to two factors: moisture and energy. All these climatic variables are modified or regulated by latitude and altitude.

2.2.1. Rainfall indices of plant productivity

Rainfall is known to be a reliable predictor of primary productivity in sub-Saharan habitats (e.g. le Houérou & Hoste 1977; Rutherford 1980; Deshmukh 1984; McNaughton 1985).

Vegetation types differ markedly in their degree of growth response to rainfall. le Houérou (1984) refers to this concept as rain-use efficiency. Rain use efficiency is defined as the rate of primary productivity per unit rainfall, or the amount of above ground phytomass produced per hectare per year, per millimeter of rain. In wetter regions where soil moisture is constantly available, few dominant plant species have physiological means to limit transpirational water loss or enhance moisture procurement via their roots. The rain use efficiency is therefore small. By contrast, dry land vegetation has numerous physiological and structural characteristics that reduce the impact of limited and irregular water supply. A number of studies have suggested that rain use efficiency is a distinguishing characteristic of vegetation types, particularly in arid and semi-arid regions (le Houérou 1984, Noy-Meir 1985). The issue is complex however, since the ratio of productivity to rainfall depends also on soil moisture retention and textural properties, land productivity and degree of land cover.

Plant evapotranspiration should ideally be used to measure plant productivity. Net primary productivity is correlated with annual actual evapotranspiration (Rosenzweig 1968; Leith & Box 1972). Potential evapotranspiration (PET), based on air temperature and day length, measures the potential amount of water released into the atmosphere from plants, through both surface evaporation, respiration and transpiration. PET is strongly dependent on temperature (Pianka 1978), and regulated by altitude, latitude and slope. In the absence of data to compute evapotranspiration, it has been suggested (le Houérou 1984), that the number of months where precipitation (in millimetres) is greater than two times the mean annual temperature (in degrees Celsius)

(P>2t) can be used as an index of productivity. Many more indices may be used (reviewed in Tuhkanen 1980), including those using temperature sums, potential evapotranspiration, precipitation-temperature relations, precipitation-evaporation relations, duration of dry conditions, and number of precipitation days. The limiting factor in all these indices is the availability of sufficiently detailed data with which to compute evapotranspiration, therefore substitute indices have to be used. In this chapter I shall investigate a range of alternative predictors of plant productivity, that will be used in subsequent chapters in the development of behavioural ecological models, in which behaviours are correlated with environmental variables.

2.2.2. Indices of seasonality

In addition to indices of productivity, the temporal distribution of rainfall is an important ecological component. These indices characterise the seasonality of the habitat, which has an effect on productivity. Variability in rainfall is inversely correlated with the amount that falls. The coefficient of variability increases from 10 to 15 percent in the rainforest, to more than 50 percent in the desert (le Houérou & Popov 1981). The relationship between rainfall variability and the amount that falls appears linear for rainfall above 100mm. The relationship does not hold for mean annual rainfalls below 100mm because the frequency distribution of rainfall is skewed (le Houérou & Popov 1981).

The number of months where rainfall is less than 50mm has been used for Africa (Dunbar 1992*b*; but see Bronikowski & Altmann 1996). This can be justified on the grounds that mean annual rainfall for sub-Saharan Africa is approximately 24.5°C, which in the formula P>2t, means that the number of months where rainfall is greater than 49°C (i.e. approx. 50mm) is a productive month. However, for central and south America, a different criterion has been suggested for defining a dry and wet month, the number of months with rainfall greater than 60mm (Clinebell *et al.* 1995). Any measures of dry season length to estimate the severity of drought experienced by plants, is only a proxy, since other environmental factors are contributory (e.g. water-retaining capacity of the

soil, insolation and temperature). Clinebell *et al.* (1995) assumed that where monthly rainfall in the tropics exceeds 100mm, it can be assumed to be exceeding PET, whereas monthly rainfall less than 60mm is below PET. These assumptions are supported by the climate diagrams in Walter & Leith (1967).

Rainfall seasonality has received relatively little attention in the climatic indices of vegetation literature. When it is used, its usefulness and accuracy have been criticised (Rutherford & Westfall 1994; Bronikowski & Webb 1996). For example, the usefulness of Simpson's index of diversity (Z) (Peet 1974) (see table 2.2), which is derived from the species diversity literature (Magurran 1988), has been questioned (Bronikowski & Webb 1996), since it does not take dry months into account. There is as yet no one index that is universally useful in all habitat types. Some indices provide insufficient variance between values for statistical tests, for example when rainfall is very low and/or even. In addition there is insufficient data on the relationships between the indices and actual plant productivity.

The quantity of production, its distribution in time and space and its predictability would all be important factors contributing to the stability of an ecosystem. Increased production will increase the number of potential niches, and thus stability. Whittaker (1970) has shown increased diversity, and hence stability with increased rainfall in tropical environments, and with increased solar input in the mid and high latitudes (fig. 3.8. Whittaker 1970).

In relation to palaeoenvironments, the distribution of stable and diverse ecosystems can indicate the degree to which different regions have been subject to climatic change during geological time. The higher latitudes are less stable and diverse than the low latitudes - which were more affected by the reduced temperatures and fluctuating environments of the Pleistocene.

2.2.3. Rainfall diversity measures for indexing seasonality

The water available to plants has typically been expressed as soil moisture, which is a direct result of effective precipitation. The water available to plants can be expressed in

a number of ways. Most simply, water availability can be characterised by an aridity index:

$H=P/(T+10)$
P = mean annual precipitation (mm)
T = mean annual temperature (°C)
(Du Martone, cited in Tuhkanen 1980).

The aridity index accounts for the inverse effect of temperature on available water. Characterising drought is important, since it emphasises the importance of water as a limiting factor during a physiologically important period. Hounam *et. al.* (1975) list more than fifty different measures of drought. One example is the Summer Aridity Index (SAI). SAI reflects moisture at a physiologically important time of year, and under conditions of high evaporative demand. It is important to note that the SAI is not strictly a 'drought index' since it refers to moisture conditions whereas drought indices reflect irregular periods of subnormal rainfall.

2.2.4. Examples of seasonality indices

In this section I shall list examples of seasonality indices and critically assess their usefulness on sub-Saharan African climate data. The aim of indices of seasonality is to indicate in one number, the distribution of rainfall across the months of the year. Markham (1970) developed a seasonality index that assumed that mean monthly rainfall values were vector quantities with both magnitude and direction. The magnitude was the amount of rain in a month, the direction was the month of the year expressed in units of an arc. The twelve monthly vectors are then added to obtain the magnitude (indicating the degree of seasonality). The direction of the vector indicated the period of seasonality. The ratio between the magnitude of the resultant vector and the total mean annual precipitation, expressed as a percentage, gave the Seasonality Index. The one drawback of this method was the method of calculation, however despite this, Markham's index is still referred to in recent literature (e.g. Linacre 1992). Therefore further seasonality indices were sought from the literature.

Bailey (1979) characterised rainfall in the form of winter concentration of rainfall (R), using the six winter months (April to September in the Southern Hemisphere, October to March in the Northern Hemisphere). Bailey (1979) defined five classes of R; strong winter ((≥ 81%), winter (61-80%), even (41-60%), summer (21-40%) and strong summer (≤ 20%). The winter concentration of precipitation as a proportion is not seen as a sensitive index on its own, but combined with the SAI assumes much greater significance. Walsh (1981) defined seasonality in the tropics in four regimes;

i. Relative seasonality

ii. Absolute seasonality

iii. Time of rainfall maximum and minimum

iv. Year-to-year reliability of rainfall.

i. Relative Seasonality

Relative seasonality is concerned with seasonal contrasts, two indices can be computed (see table 2.1).

Table 2.1. Seasonality indices.

Index	Formula	Range of index values*
Seasonality ratio (SR)	$\frac{x\max - x\min}{R}$	0.00-1.00
Seasonality index (SI)	$\frac{\sum_{n=12}^{n=1}\left\lvert x_n - \frac{R}{12}\right\rvert}{R}$	0.00-1.83

*High index value, indicates a more seasonal environment (greater contrasts between seasons).
xmax = mean rainfall of wettest month; xmin = mean rainfall of driest month; R = mean annual rainfall; xn = mean rainfall of month; n = month, where 1 = January, 2 = February etc.

The seasonality ratio (SR) is the ratio of the range of the mean monthly rainfall, and the mean annual rainfall. The SR only takes into account the wettest and driest months. The seasonality index (SI) (Walsh 1981) is the sum of the absolute deviations of mean monthly rainfall from the overall mean, divided by mean annual rainfall. The SI can have a value of 0.00 (all months have equal amount of rain) to 0.83 (all rain concentrated in one month).

ii. Absolute seasonality

It is important to define the length of the dry period; the period over which the soil has dried out, and the vegetation has entered its dormant phase. A dry period is one where there is insufficient water to meet the potential needs of plants as measured by potential evapotranspiration (PET). Because it is difficult to calculate PET directly, alternative indices have been sought. The number of months with rainfall less than 50mm is commonly used (Schmidt 1928; Miller 1953; Lewis 1975). However, water deficits arise in the tropics at monthly rainfalls well in excess of 50mm, therefore some view 100mm as more realistic (e.g. Mohr *et al.* 1972; Bronikowski & Webb 1996). Bowden (1964) used the number of months with precipitation less than 25mm as the dry season, however this definition is infrequently used, since it is too stringent a cut-off value. The approach of using the number of dry months is reasonable in those parts of the world where temperature remains fairly constant throughout the year.

iii. The timing of rainfall between maxima and minima

Seasonality may simply be expressed qualitatively as the number of peaks and troughs in rainfall throughout the year (see section 2.3.3).

iv. Reliability and seasonality

Rainfall reliability is reflected in the variation of rainfall for the same month as between years. Reliability tends to be lower, the lower the mean annual rainfall, and lower when absolute and relative seasonality is high. The more marked the seasonality, the less reliable the rainfall is during the rainy season; there are at present no quantitative techniques to assess rainfall reliability.

2.3.3. DIV: a new rainfall diversity index

The criticisms of existing indices focus on whether there is sufficient variance in the data used to compute the indices, to sufficiently distinguish habitat types. Bronikowski & Webb (1996) found Simpson's index of diversity insufficient at describing the diversity of

rainfall found at Amboseli. This could in part be attributed to the low mean annual rainfall (1982-1991, 335mm; Bronikowski & Altmann 1996). The comparative socioecological models in subsequent chapters will use data from populations from a wide geographic area. Therefore the rainfall diversity index used should be appropriate for both low and high rainfall sites.

A new index was developed based on the exact randomisation methods (Sokal & Rohlf 1984; Manly 1991), using complete enumeration (see Sokal & Rohlf 1984). The difference between all possible pairwise comparisons between 12 mean monthly rainfall values (in millimeters) was computed. To illustrate the computation of the index, a matrix could be constructed, 12 months by 12 months, with rainfall values for each month for a particular site in the row and column headings (fig. 2.1)

Figure 2.1. Matrix to illustrate calculation of the DIV index of rainfall diversity.

	Jan 100	**Feb** 35	**Mar** 55	**Apr** 100	**May** 100	**Jun** 10	**Jul** 5	**Aug** 0	**Sep** 0	**Oct** 50	**Nov** 75	**Dec** 100
Jan 100	*											
Feb 35	65	*										
Mar 55	45	20	*									
Apr 100	0	65	45	*								
May 200	100	165	145	100	*							
Jun 10	90	25	45	90	90	*						
Jul 5	95	30	50	95	95	5	*					
Aug 0	100	35	55	100	100	10	5	*				
Sep 0	100	35	55	100	100	10	5	0	*			
Oct 50	50	15	5	50	50	40	45	50	50	*		
Nov 75	25	40	20	25	25	65	70	75	75	25	*	
Dec 100	0	35	45	0	0	90	95	100	100	50	25	*

*** = No difference, comparing the same monthly rainfall.**
Mean of differences (n = 66), = 54.25
DIV = Mean of differences / n, = 54.25 / 66 = 0.821
DIV = 0.821

The mean of these 66 comparisons was then found, which was the DIV index. Additionally, the pairwise differences between mean monthly rainfall values could then be plotted to illustrate the modality of rainfall distribution. The DIV index could distinguish between unimodal, and bimodal patterns of rainfall distribution.

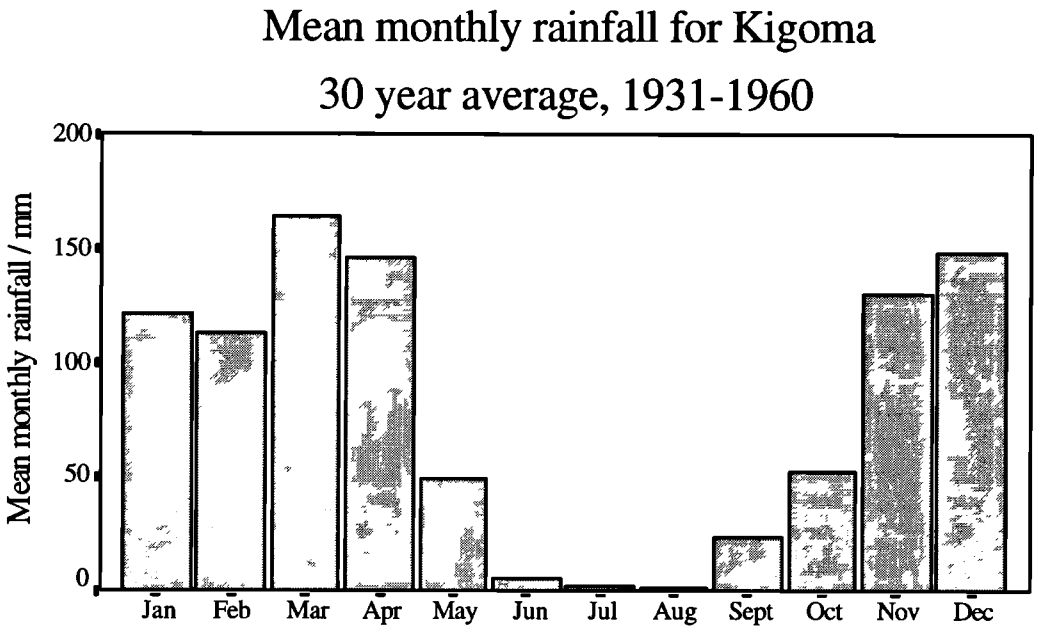
Tropical rain forests occur between 20°N and 20°S (Malenky 1990). Within this zone, rainfall is predominantly convectional and peaks at the same time as the inter-tropical convergence zone (ITCZ). The ITCZ is a low pressure trough that oscillates predictably north and south of the equator. Therefore sites near the equator tend to have

two peaks of rainfall, corresponding to the ITCZ passing between its summer and winter extremes. Sites close to either extreme of the ITCZ have a single rainy and dry season, longer in duration than the dry seasons at sites closer to the equator.

The DIV index was tested on several African climate databases. Figures 2.2 and 2.3 use data from Hulme (CRU0092.DAT, 1993). The database CRU0092.DAT is an historical monthly precipitation dataset for global land areas from 1900 to 1992, gridded at 2.5° by 3.75°, with on average 90 years of data available for each site. The database is both comprehensive and accurate. However because the data are provided in grid-squares they are not accurate for pinpointing rainfall in specific sites. Figures 2.2 and 2.3 compare data from a bimodal rainfall distribution (fig. 2.2) and unimodal distribution (fig. 2.3). Frequency histograms of all pairwise differences between 12 months of data reflect this rainfall distribution pattern.

Figure 2.2. Histograms to illustrate the modality of rainfall at Kigoma, Tanzania. (data from Hulme 1993) (A), and the rainfall diversity index DIV, calculated from this data (B).

[A]



[B]

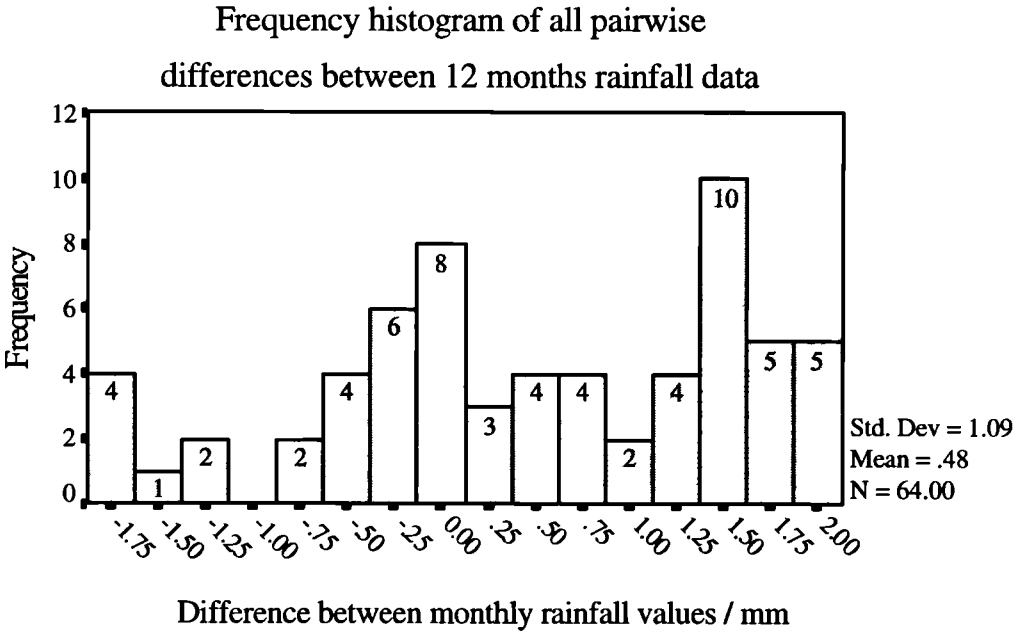
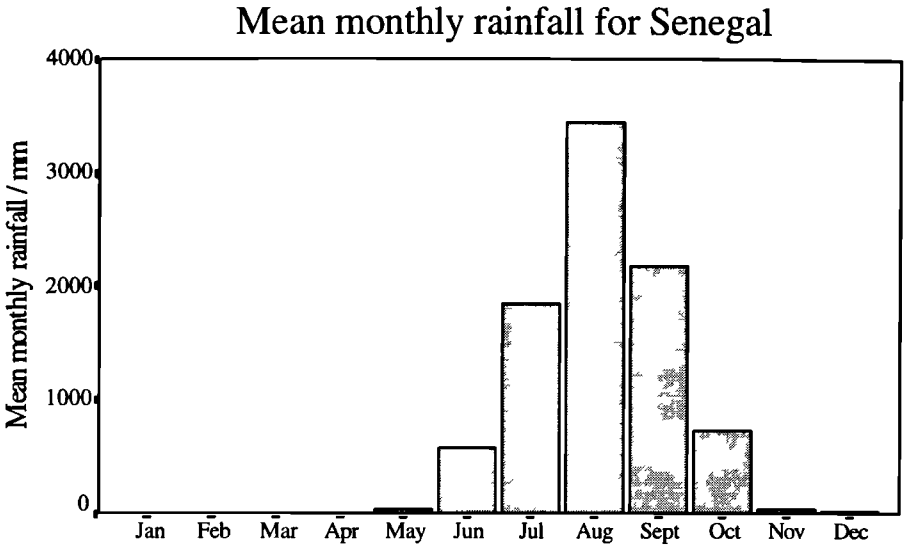
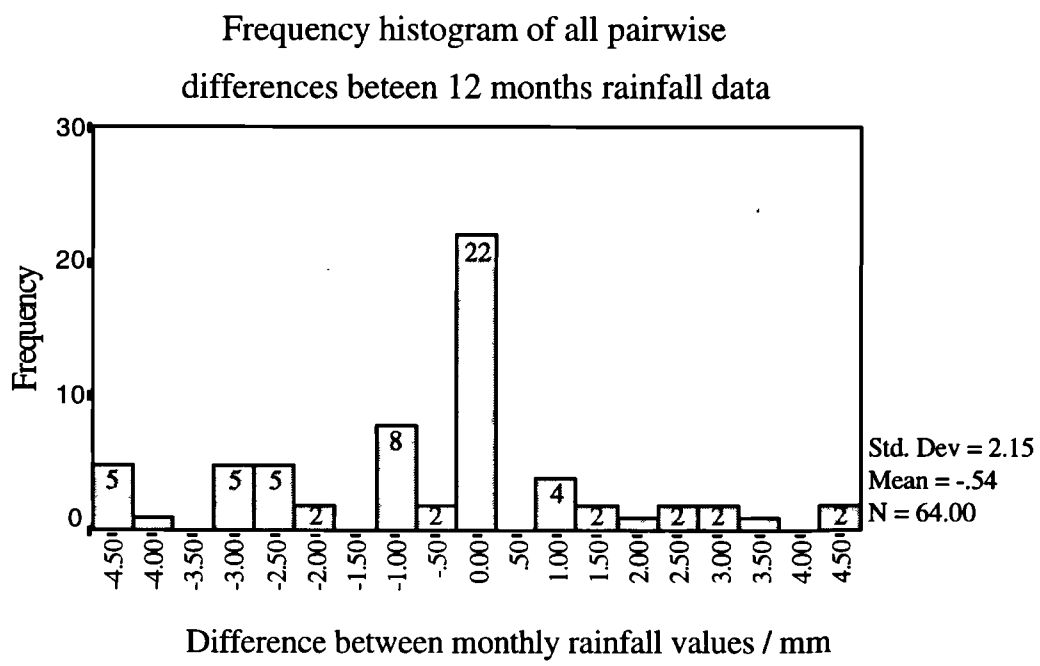


Figure 2.3. Histograms to illustrate the modality of rainfall at Mount Assirik, Senegal (data from Hulme 1993) (A), and the rainfall diversity index DIV, calculated from this data (B).

[A]



[B]



2.3. AN ASSESSMENT OF RAINFALL DIVERSITY INDICES

A climatic year can be defined in two ways, a calendar year, or an ecological year (starting in either the wet or dry season). The calendar year is used in all published meteorological records referred to, and is therefore used here. Defining a climatic year on ecological grounds, (starting the year in a wet or dry season) is beneficial in southern monsoonal climates and northern Mediterranean climates, where the dry season occurs mid-year. This avoids dividing a wet-season across consecutive years.

In this section I shall compare rainfall diversity indices, and assess the usefulness of the DIV index, developed in section 2.3.3. The diversity indices in table 2.2 measure the evenness of rainfall (the spread of rainfall across the months of a given year). The formulas to measure rainfall evenness come from the species diversity literature. Species diversity indices reflect both the number and abundance of species (Magurran 1988). In the example of rainfall, the number of 'species' is the number of months in the year (a constant, 12). The proportion of the overall sample, is represented here by the proportion of annual rainfall in each month. A diversity index of 1 indicates complete evenness, in otherwords, equal rainfall falling in each month. A diversity index of zero indicates complete unevenness in the distribution of rainfall across the 12 months. Species diversity indices fall into two categories; dominance measures (Simpson, McIntosh and Berger-Parker indices), and information theory measures (Shannon and Bruillouin indices) (see table 2.2). Dominance measures weight the diversity index towards the dominant month (the month with the most rainfall). The advantage of dominance measures is that if the rainfall increases in one month, and the rest remain constant, a dominance measure will decrease faster than a non-dominance measure (i.e. the more uneven the rainfall will seem). If the index decreases, this characterises uneven rainfall. By contrast, information theory measures use the natural logarithm of monthly proportional rainfall.

Ultimately, the choice of rainfall diversity index should be based on how useful the index is in behavioural ecological models. Climatic variables may affect animals directly (e.g. thermal stress), or indirectly (how rainfall indexes availability of resources

for animals). In subsequent chapters (chapters 3 and 4) I shall be using an index of seasonality to correlate with baboon (chapter 3) and chimpanzee (chapter 4) behaviour.

Independently from the behavioural data, the choice of index will be based on how sensitive it is to small changes in rainfall, and that the value of the index has the greatest spread under different rainfall regimes. The indices to be evaluated are listed in tables 2.1 and 2.2.

Table 2.2. Diversity indices.

Index*	Formula	Range of index value**	ref.
Shannon[1]	$D = -\frac{\sum(p_i \ln(p_i))}{\ln(12)}$	0.00-1.00	1
Bruillouin[1]	$D = \frac{\ln(N!) - \sum \ln(n_i)}{\ln(N!) - \{(S-r)\ln[(N/S)!]\} - \{r \ln[(N/S)+1]!\}}$	0.00-1.00	1
Simpson[1]	$D = 1 - \sum(p_i{}^2)$	0.00-0.92	1
McIntosh[1]	$D = \frac{N - \left(\sum n_i^2\right)^{0.5}}{N - N^{0.5}}$	0.00-1.00	1
Berger-Parker[1]	$D = 1 - (n_{\max} / N)$	0.00-0.92	1
Seasonality Ratio (SR)[2]	$\frac{x\max - x\min}{N}$	0.00-1.00	2
Seasonality Index (SI)[2]	$\frac{\sum_{n=12}^{n=1} \left\lvert x - \frac{N}{12} \right\rvert}{N}$	0.00-0.83	2
DIV[3]	see section 2.3.3.	0.16-2.00	3

*References: (1) Magurran (1988); (2) Tuhkanen (1980); (3) see section 2.3.3.
** High index value indicates a more seasonal environment (greater contrasts between seasons).
n_i = rainfall per month, N=rainfall per year, p_i = proportion of rainfall per month, S = number of months = 12, $x$max = mean rainfall of wettest month, $x$min = mean rainfall of driest month, x_n= mean rainfall of month n, where n= month 1 = January, 2 = February etc.

Following Bronikowski & Webb (1996), rainfall regimes were simulated (see table 2.3), and diversity indices computed for each simulated rainfall regime.

Table 2.3. Simulations of rainfall diversity indices

Month	Rainfall / mm										
January	100	0	0	0	0	0	0	0	0	0	0
February	100	0	0	0	0	0	0	0	0	0	0
March	100	100	0	0	0	0	0	0	0	0	0
April	100	100	100	0	0	0	0	0	0	0	0
May	100	100	100	100	0	0	0	0	0	0	0
June	100	100	100	100	100	0	0	0	0	0	0
July	100	100	100	100	100	100	0	0	0	0	0
August	100	100	100	100	100	100	100	0	0	0	0
September	100	100	100	100	100	100	100	100	0	0	0
October	100	100	100	100	100	100	100	100	100	0	0
November	100	100	100	100	100	100	100	100	100	100	0
December	100	100	100	100	100	100	100	100	100	100	100
Total	1200	1000	900	800	700	600	500	400	300	200	100
Index*											
Shannon	1.00	0.93	0.88	0.84	0.78	0.72	0.65	0.56	0.55	0.44	0
Bruillouin	1.00	0.93	0.90	0.85	0.80	0.74	0.68	0.60	0.49	0.33	0
Simpson	0.92	0.90	0.90	0.87	0.86	0.83	0.80	0.75	0.67	0.50	0
McIntosh	1.00	0.96	0.94	0.91	0.53	0.83	0.78	0.70	0.60	0.41	0
Berger-Parker	0.92	0.90	0.89	0.88	0.86	0.83	0.80	0.75	0.67	0.50	0
DIV	0.16	0.49	0.65	0.80	0.94	1.06	1.16	1.23	1.21	1	2
CV	0	46.71	60.30	73.85	88.27	104.45	123.58	147.71	180.91	233.55	346.41
SD	0	38.92	45.22	49.24	51.49	52.22	51.49	49.24	45.23	38.92	28.87
SI	0	0.33	0.40	0.46	0.53	0.60	0.67	0.73	0.79	0.86	0.89
SR	0	8.33	8.33	8.33	8.33	8.33	8.33	8.33	8.33	8.33	0

* See table 2.2. for definitions of diversity indices.

To assess the spread of index values across rainfall regimes, the indices are plotted in figures 2.4.a & b.

Conclusion

Of the evenness indices, the Shannon and Bruillouin indices showed the best spread of values. The Simpson and Berger-Parker indices were very similar, with a lower spread than the Shannon index. The drop in the McIntosh index at 5 months with zero rainfall, illustrates the fact that the McIntosh index is dependent on the overall amount of rainfall. Indices that use proportional rainfall circumvent this problem. The Bruillouin index had a similar spread to the Shannon index, also ranging from 0 to 1. However, the Bruillouin index was less suitable at high rainfall values. Based on a similar analysis, Bronikowski & Webb (1996) concluded that the Shannon index was the most suitable index, being both simple to calculate, and having a good spread of values across a range of rainfall values. The Simpson index was favoured by Dunbar (1992*b*) to characterise rainfall evenness in a study of the correlation between meteorological and behavioural variables in baboons, because it is independent of the quantity of rainfall. The value of the Simpson's index is always less than 1, because it only calculates evenness across months with rainfall. For example, if there were 12 months of equal rainfall, the minimum value

Figure 2.4.a. Species diversity indices of rainfall diversity

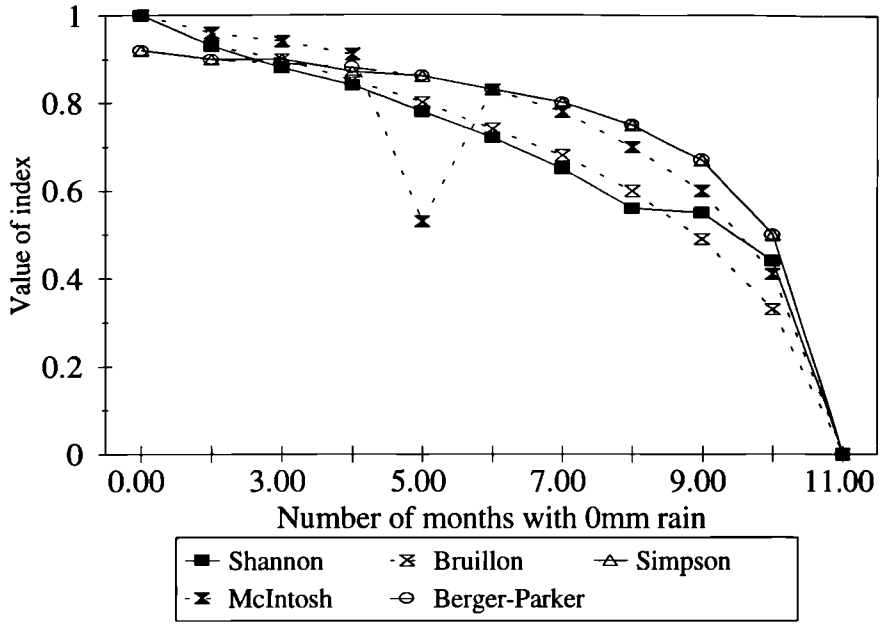
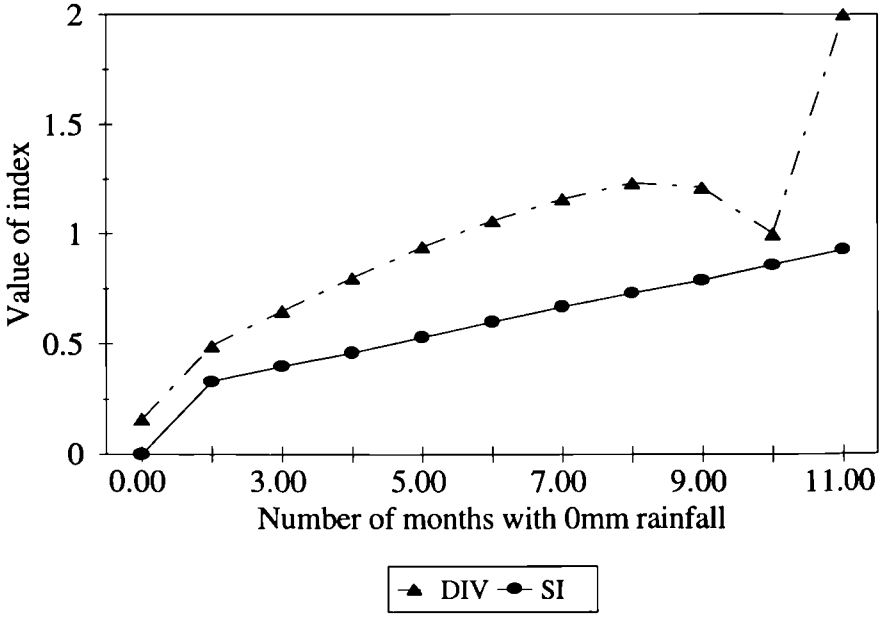


Figure 2.4.b. Diversity indices of rainfall diversity



of Simpson's index is 11/12 or 0.917. And in a year with 6 months rainfall, and 6 dry months, the maximum value of Simpson's index is 5/6 or 0.83. Simpson's index still provides a good spread of values across months, and is useful, so long as the limiting values are taken into account.

The seasonality index (SI) and new diversity index (DIV) have the reverse trend in values to the species diversity indices. A low value characterises even rainfall, a high index represents more seasonal rainfall. Similar to the McIntosh index, DIV is dependent on the overall amount of rainfall, however it is advantageous in having the widest spread of values. The seasonality index (SI), also successfully distinguishes between rainfall regimes.

2.4. TESTING RAINFALL DIVERSITY INDICES

The preceding analysis has independently assessed the usefulness of different rainfall diversity indices. However, these indices are only useful in so far as they accurately characterise habitat productivity. In this section I shall assess how well indices of rainfall seasonality correlate with direct and indirect measures of habitat productivity. Correlations between climatic variables for the climatic databases analysed in this chapter are presented in appendix I.

2.4.1. Thornthwaite and Mather database.

The aim of this analysis was to validate two of the indices used in further analyses in this thesis (chapters 3 & 4). The two indices tested in detail were; Simpson's index of rainfall diversity (Z), and the statistic based on the exact randomisation test (DIV). The advantage with Thornthwaite & Mather's (1962) data base is that it gives values for evapotranspiration, which are known to index plant primary productivity directly.

Variables used in the comparisons

The following climatic variables were recorded; mean annual temperature / °C; mean annual rainfall / mm; number of months with less than 50mm or 100mm rainfall; the

number of months where mean monthly rainfall / mm was greater than twice the mean monthly temperature (°C), P>2t. In addition to monthly rainfall, water surplus (S) and water deficit (D) are listed. Water surplus and deficit are related to potential evapotranspiration. Both actual, and potential evapotranspiration are listed (AE and PE respectively). AE and PE will be equal so long as the soil moisture content or storage is at field capacity. When water storage drops below the water holding capacity of the soil, the actual loss of water from the soil drops below the potential rate proportionally. For example, when the amount of water stored in the soil is 75 percent of the water holding capacity, the actual evapotranspiration will be 75 percent of the potential. Water surplus (S) is defined as the excess precipitation (P-PE) which occurs when the soil moisture storage equals the water holding capacity of the soil. Water deficit (D) is the difference between potential and actual evapotranpsiration in any month.

Two-tailed Spearman rank correlations were computed (see appendix I) on climatic variables listed in Thornthwaite & Mather (1962). Data were sampled randomly from 189 weather stations randomly distributed in sub-Saharan Africa. Least squares regressions were computed on those variables significantly correlated with one another (see figures 2.5 a to m).

Stepwise regression equations were computed to establish the key predictors of each of the indices of seasonality; DIV, Simpson's (Z), number of months with less than 50mm, or less than 100mm rainfall.

Table 2.4. Multiple regression equations from climate data presented in Thornthwaite & Mather (1962)

Multiple regression equation*	R^2	*F(df)*	*P*
$DIV = .474925 + .002055(D)$	.98	137.74(1,3)	0.0013
$Z = .950058 - 3.80336E\text{-}04(D)$	.94	45.16(1,3)	0.0067
$Mo50 = -19.14244 + 16.875(Z) + 8.87\ (DIV)$	.99	1567.08(2,2)	0.0006
$Mo50 = 13.398 - .004348(AE)$	.95	54.13(1,3)	0.0052
$Mo100 = 17.3407 - .0052(AE)$	.99	266.70(1,3)	0.0005

* *DIV* = Rainfall diversity index; *D* = water deficit (mm/yr; see text); *Z* = Simpson's index of rainfall diversity; *Mo50* = number of months with <50mm rain; *Mo100* = number of months with <100mm rain; *AE* = annual evapotranspiration (mm/yr; see text).

The diversity index (DIV), which is highly correlated with P>2t is highly correlated with water deficit (D), indicating a dry, non-growing season. Therefore the DIV index does tell us something about the dry, non-growing period. The same applies for a step-wise multiple regression with Z as the independent variable; Simpson's index of diversity does seem to index the extent of the dry season, and therefore productivity. The number of months < 50mm rain and less than 100mm rain correlates with indices of productivity. Two equations are shown, because the first equation contains variables known to be correlated with Mo50, and therefore violates the condition of collinearity in step-wise regression. The number of months with less than 50mm correlates highly with annual evapotranspiration. The relationship is negative; the more months >50mm the higher the AE. The significant regressions in figures 2.5.a to m are summarised in table 2.5.

Table 2.5. Significant least squares regression equations from climate data in Thornthwaite & Mather (1962), (see figures 2.5.a to h).

Multiple regression equation*	Figure 2.2	R^2	*F(df)*	*P*
D = -469.66 + 826.62 (*DIV*)	a	0.67	155.57 (1,187)	0.00
D = 684.86 - 0.34 (*AE*)	b	0.52	17.44 (1,47)	0.0001
AE = 1615.31 - 126.12 (*Mo50*)	c	0.62	28.84 (1,47)	0.00
AE = 1853.96 - 120.19 (*Mo100*)	d	0.72	50.95 (1,47)	0.00
Mo50 = -2.53 + 7.14 (*DIV*)	e	0.83	421.51 (1,187)	0.00
Mo100 = -0.26 + 6.59 (*DIV*)	f	0.71	200.71 (1,187)	0.00
AE = 1822.25 - 802.46 (*DIV*)	g	0.49	14.74 (1,47)	0.0004
D = -173.18 + 114.76 (*Mo50*).	h	0.80	339.72 (1,187)	0.00
Z = 1471.91 - 185.56(*AE*)	i	0.35	6.84 (1,187)	0.0119
Z = -2495.75 + 2449.03 (*D*)	j	0.59	327.72 (1,187)	0.00
Z = -2.712 + 3.267 (*DIV*)	k	0.79	327.72 (1, 187)	0.00
Z = -16.05 + 19.69(*Mo100*)	l	0.52	67.80 (1, 187)	0.00
Z = -17.55 + 19.24(*Mo50*)	m	0.60	106.06 (1, 187)	0.00

* *D* = rainfall deficit (mm); *DIV* = rainfall diversity index; *AE* = annual evapotranspiration (mm); *Mo50* = number of months with rainfall less than 50mm rain; *Mo100* = number of months with less than 100mm rain; *Z* = Simpson's index of rainfall diversity.

Rainfall diversity index is highly correlated with water deficit. Water deficit defines those periods where there is insufficient ground water to support plant growth. This correlation is important as it clearly shows the relevance of DIV as an index of plant productivity. Water deficit is negatively correlated with annual evapotranspiration (AE). The significant relationship supports the assumption that water deficit indexes the non-growing period. Annual evapotranspiration is negatively correlated with the number of months with less than 50mm rainfall (Mo50). Mo50 is therefore a good approximation

of plant productivity. Similarly the number of months with less than 100mm rainfall (Mo100) is also correlated with annual evapotranspiration. The number of dry months is significantly correlated with water deficit. Both variables are indicators of the non-growing season for plants, where there is insufficient water to sustain plant growth. There is a strongly significant correlation between the index DIV and number of dry months (Mo50 or Mo100). Since we know that the number of dry months is strongly correlated with annual evapotranspiration, the relationship between DIV and annual evapotranspiration was expected.

Conclusion

The Thornthwaite & Mather database showed that the newly derived rainfall diversity index DIV, was successful in predicting plant productivity. The results show that DIV is related to both direct (annual evapotranspiration) and indirect (Mo50, Mo100) measures of plant productivity. One drawback with the database was the lack of temperature data. As a consequence, the index P>2t could not be compared to direct measures of plant productivity.

Figure 2.5. Least squares regression plots of climatic data from Thornthwaite & Mather (1962). n = 189 weather stations, randomly sampled from sub-saharan Africa.

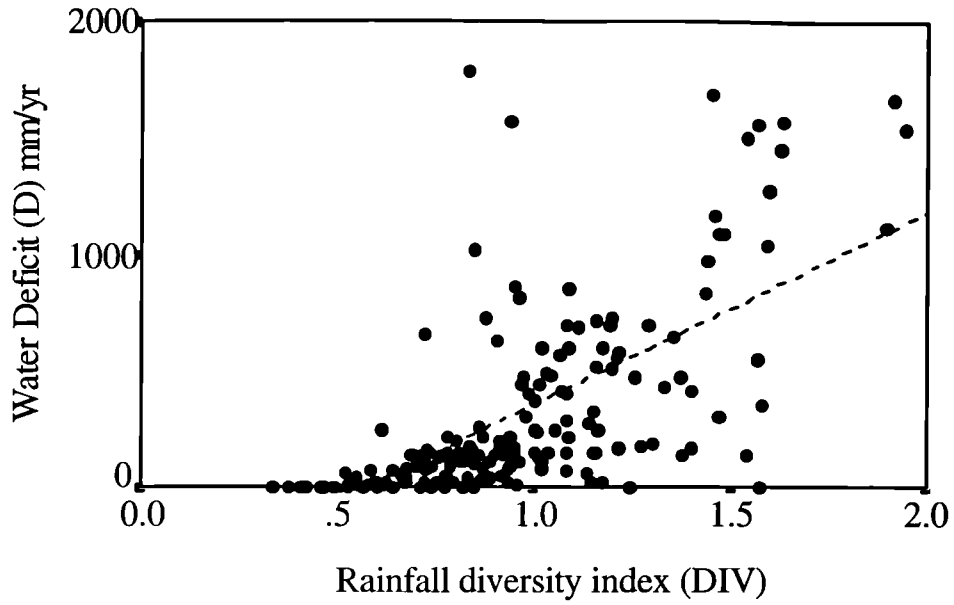


Figure 2.5.a. Water deficit against rainfall diversity.
D = -469.66 + 826.62 (DIV). (r^2 = .67; F = 155.57; df = 1, 187; p = 0.00)

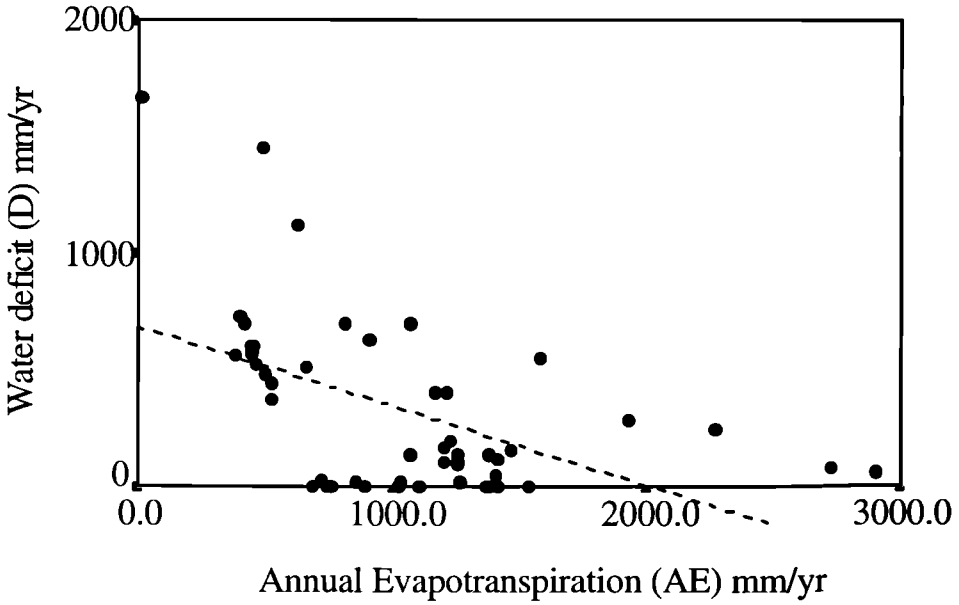


Figure 2.5.b. Water deficit against annual evapotranspiration
D = 684.86 - 0.34 (AE). (r^2 = 0.52; F = 17.44; df = 1,47; p = 0.0001)

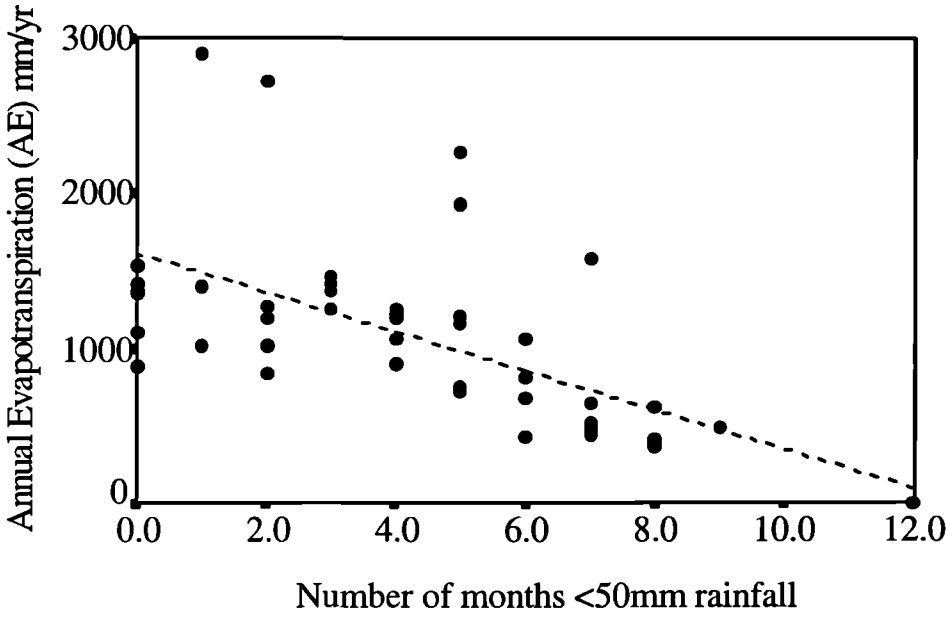


Figure 2.5.c. Annual Evapotranspiration against number of dry months.
AE = 1615.31 - 126.12 (MO50). (r^2 = .62; F = 28.84; df = 1,47; p = 0.00).

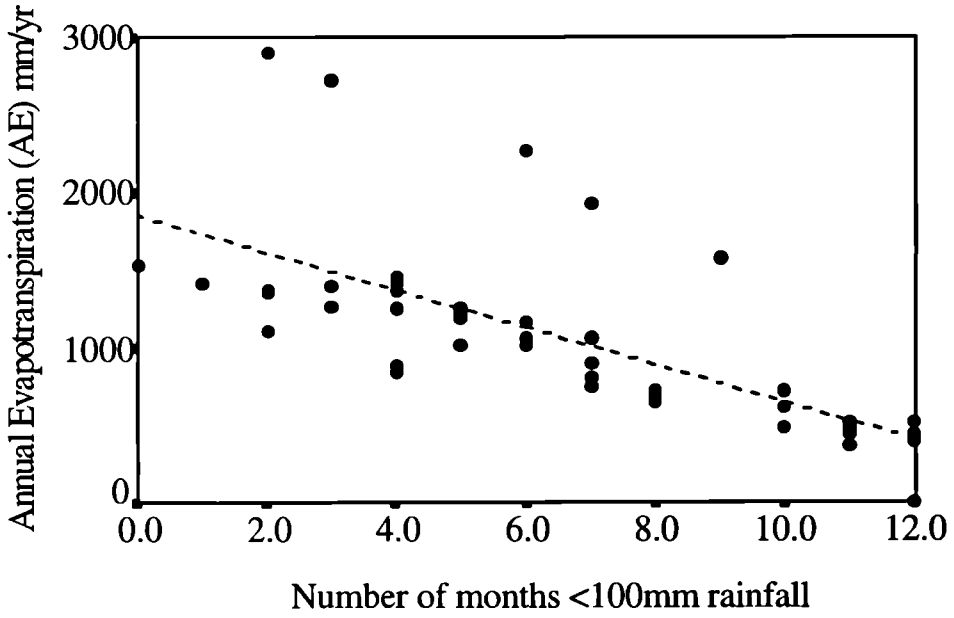


Figure 2.5.d. Annual Evapotranspiration against number of dry months.
AE = 1853.96 - 120.19 (MO100). (r^2 = .72; F = 50.95; df = 1, 47; p = 0.00)

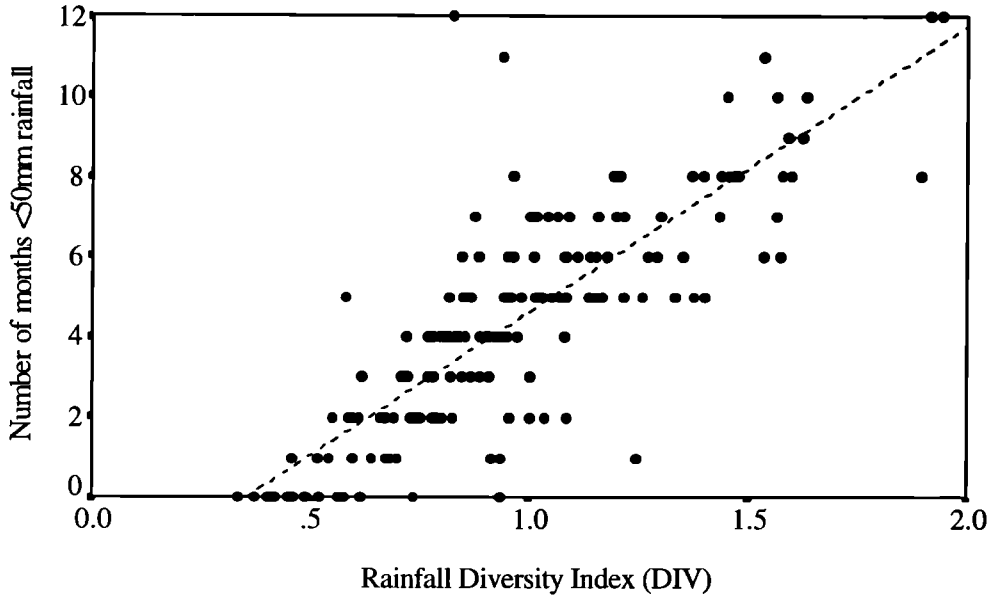


Figure 2.5.e. Number of dry months against rainfall diversity.
MO50 = -2.53 + 7.14 (DIV). (r^2 = .83; F = 421.51; df = 1, 187; p = 0.000)

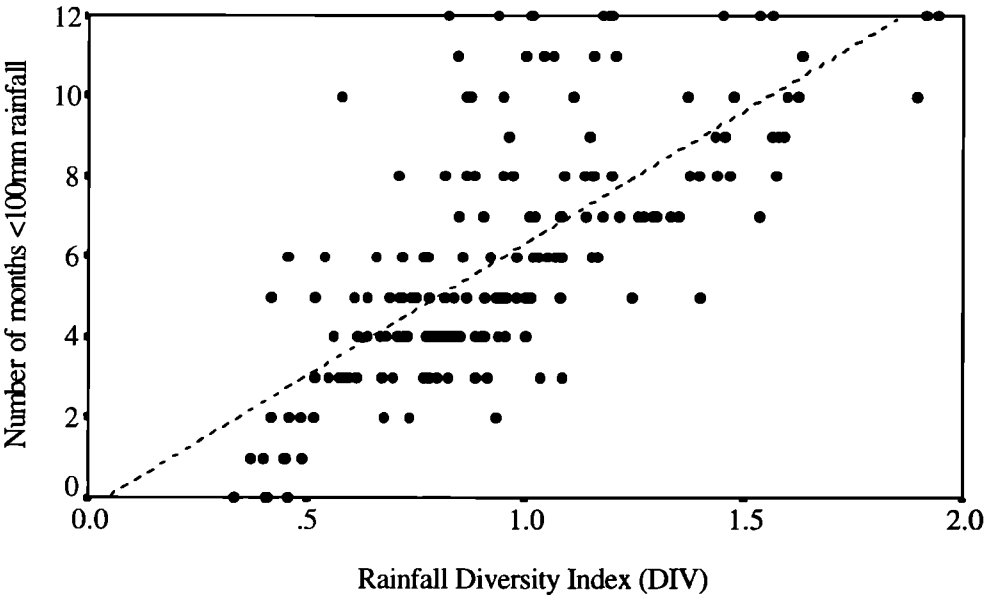


Figure 2.5.f. Number of dry months against rainfall diversity.
MO100 = -0.26 + 6.59 (DIV). (r^2 = .71; F = 200.71; df = 1, 187; p = 0.00)

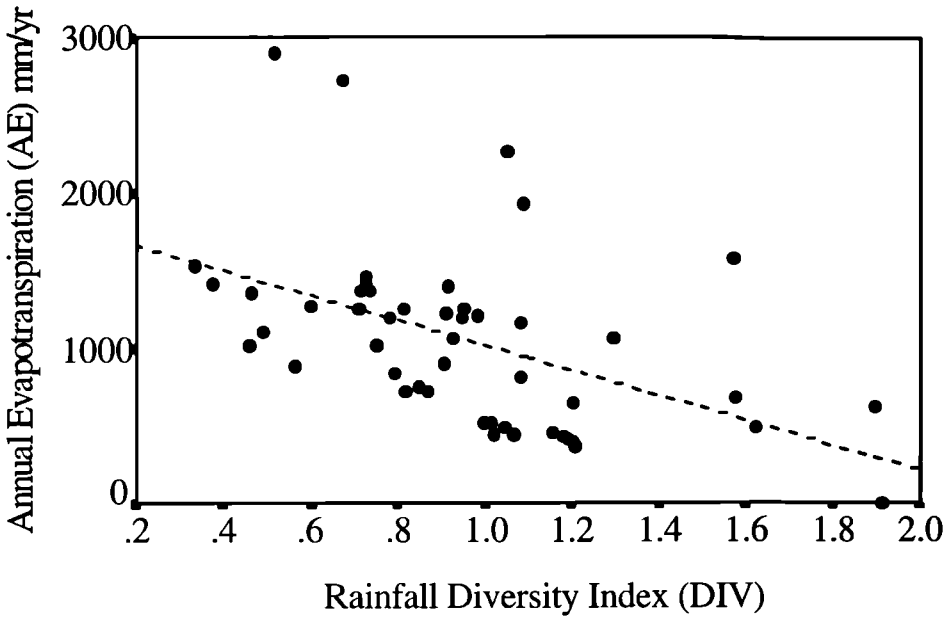


Figure 2.5.g. Annual evapotranspiration against rainfall diversity.
AE = 1822.25 - 802.46 (DIV). (r^2 = .49; F = 14.74; df = 1,47; p = 0.0004)

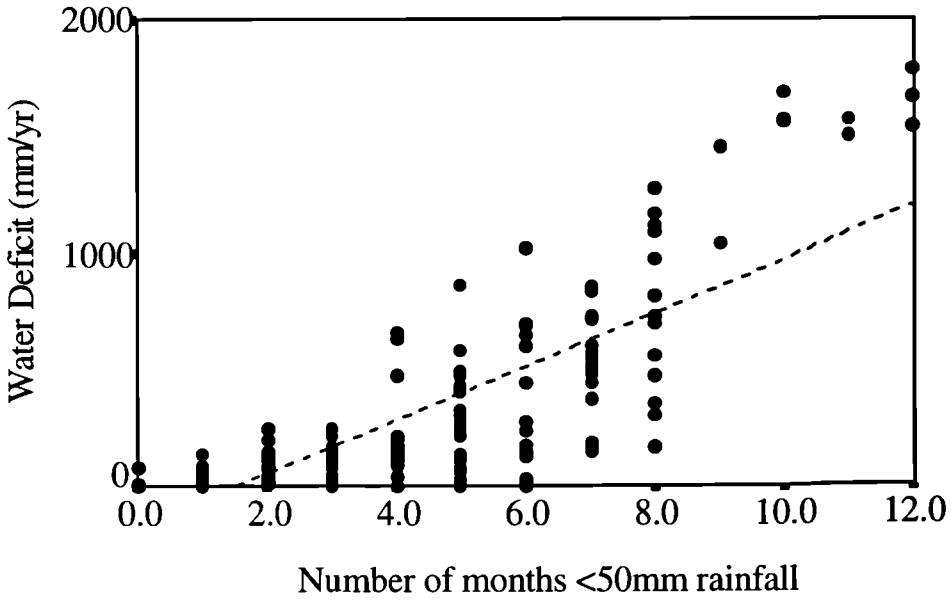


Figure 2.5.h. Water deficit against number of dry months.
D = -173.18 + 114.76 (MO50). (r^2 = .80; F = 339.72; DF = 1,187; P = 0.000)

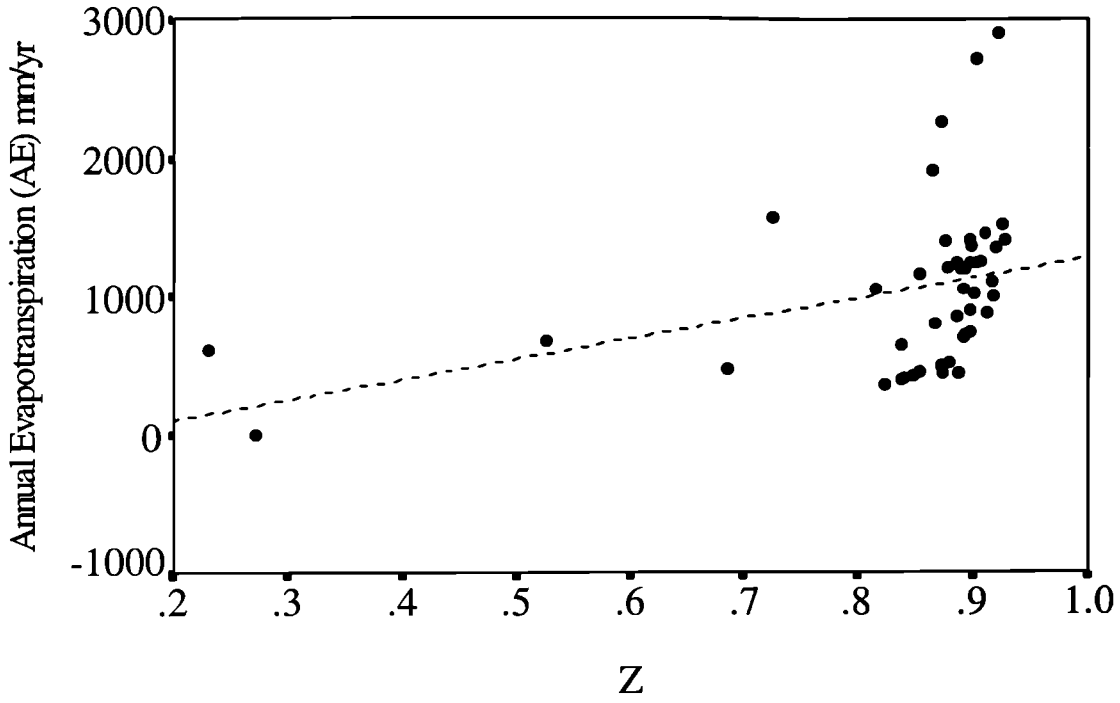


Figure 2.5.i. Annual evapotranspiration against Simspon's index of rainfall diversity
Z = 1471.91 - 185.56(AE). (r^2 = .35; F = 6.84; DF = 1,187; P = 0.0119)

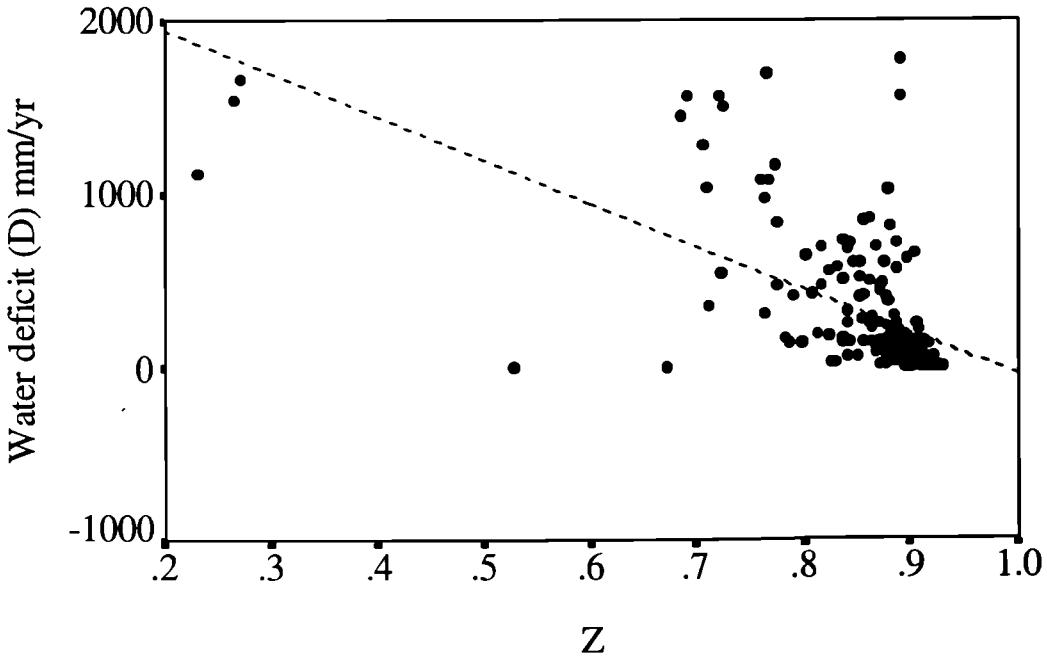


Figure 2.5.j. Water deficit against Simpson's index of rainfall diversity.
Z = -2495.75 + 2449.03 (D) (r^2 = .59; F = 327.72; DF = 1,187; P = 0.000)

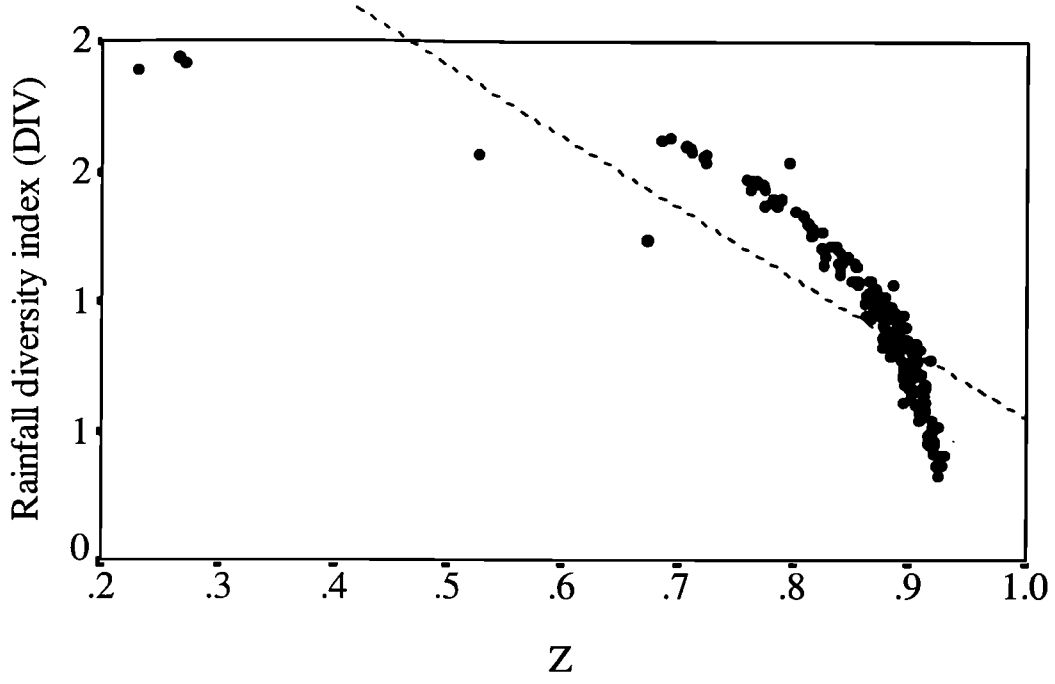


Figure 2.5.k. Rainfall diversity index (DIV) against Simspon's index of rainfall diversity Z = -2.712 + 3.267 (DIV). (r^2 = .79; F = 327.72; DF = 1,187; P = 0.000)

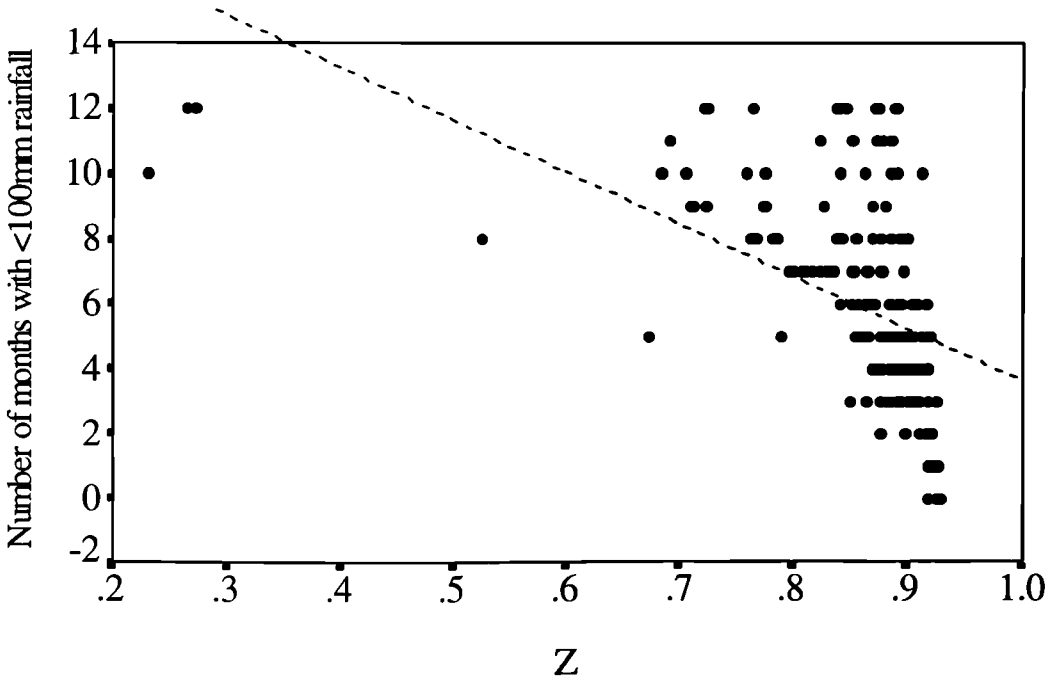


Figure 2.5.l. Number of months <100mm rain against Simspon's index of rainfall diversity Z = -16.05 + 19.69(MO100). (r^2 = .52; F = 67.80; DF = 1,187; P = 0.000)

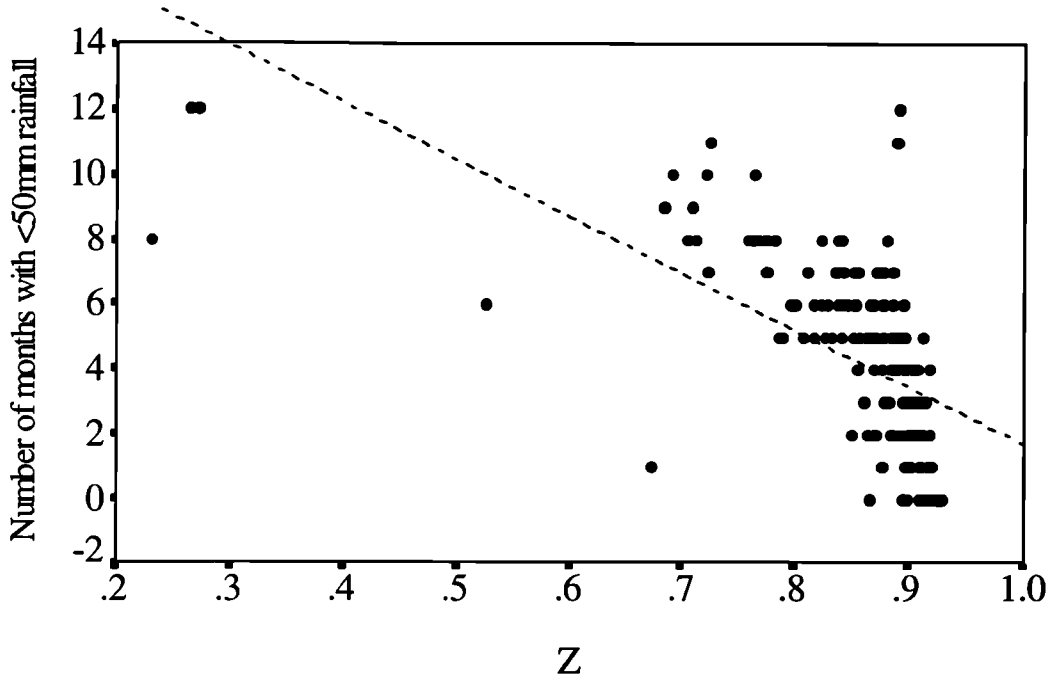


Figure 2.5.m. Number of months <50mm rain against Simspon's index of rainfall diversity Z = -17.55 + 19.24(MO50). (r^2 = .60; F = 106.06; DF = 1,187; P = 0.000)

2.4.2. Le Houérou & Popov (1981) database

The database consists of 395 weather stations, randomly distributed in sub-Saharan Africa. The advantage of this database was the availability of direct measures of plant productivity, annual evapotranspiration. The database lists data on evapotranspiration, which is presented in three ways; annual evapotranspiration, 0.35 × Potential Evapotranspiration (PET), and 0.5 × PET. One third PET corresponds very closely to the water requirements of most African crops during the days immediately after sowing, namely at the beginning of the rainy season. 0.5 × PET also describes the threshold growing period for African crops (le Houérou & Popov 1981). In West Africa, these formulas result in a monthly rainfall of 50-55mm (1.6-1.8mm/day) as the threshold of the growing season. This supports the use of the threshold, Mo50 to define a growing season.

Figures 2.6. a to c. illustrate significant regressions between the index P>2t and three measures of plant evapotranspiration. Regression equations are tabulated in table 2.6.

Table 2.6. Significant least squares regression equations from climate data in Le Houérou & Popov (1981).

Multiple regression equation*	Figure 2.4	R^2	*F(df)*	*P*
P>2t = 13.41 - 0.004 (*ANPET*)	a	0.63	258.7 (1, 392)	0.00
P>2t = 0.12 + 0.99 (*PET35*)	b	0.99	36017.58 (1, 393)	0.00
P>2t = 0.65 + 0.98 (*PET5*)	c	0.97	5697.52 (1, 393)	0.00

* *P>2t* = number of months where rainfall (in mm) is greater than twice the mean annual temperature (in °C); *ANPET* = annual potential evapotranspiration; *PET35* = 0.35 × PET (potential evapotranspiration); *PET5* = 0.5 × PET.

Conclusion

Analyses from the le Houérou & Popov data base support the use of P>2t as good proxy index of plant productivity. The advantage of this index is its ease of calculation, from data that is widely available.

Figure 2.6. Least squares regression plots of climatic data from Le Houerou & Popov (1980). N = 395 weather stations.

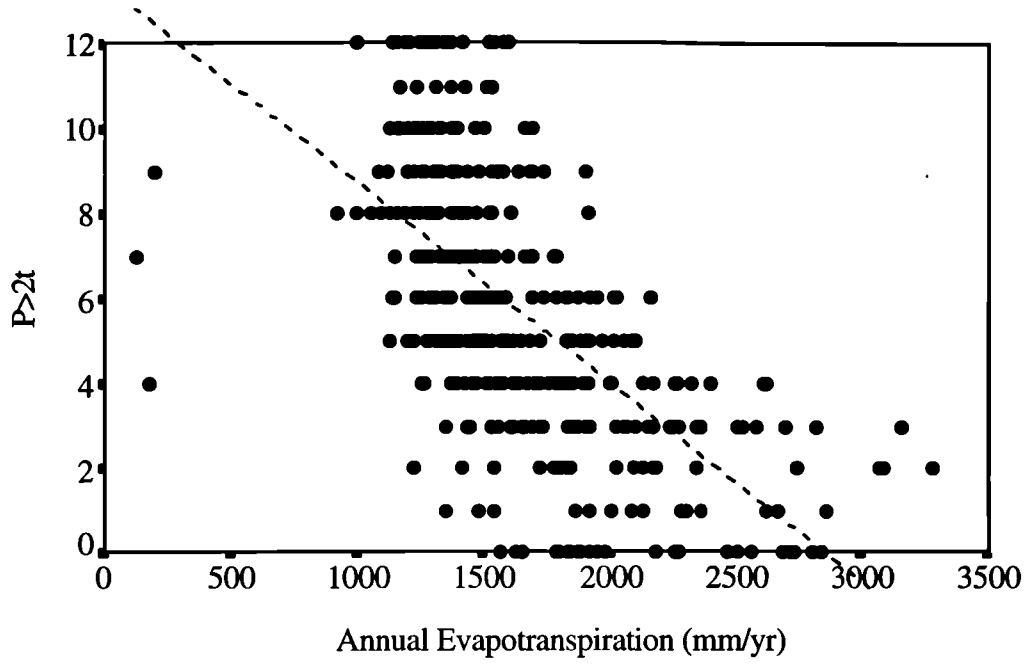


Figure 2.6.a. P>2t against annual evapotranspiration.

P>2t = 13.41 - 0.004 (ANPET). (r^2 = 0.63; F = 258.17; df = 1, 392; p = 0.00)

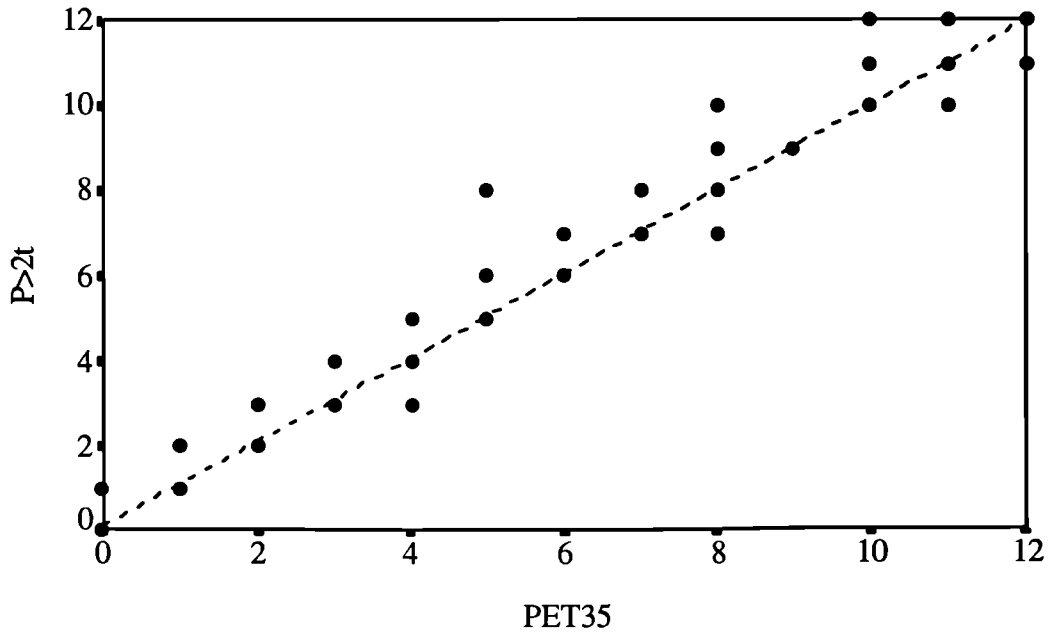


Figure 2.6.b. P>2t against PET35.

P>2t = 0.12 + 0.99 (PET35). (r^2 = 0.99; F = 36017.58; df = 1, 393; p = 0.00)

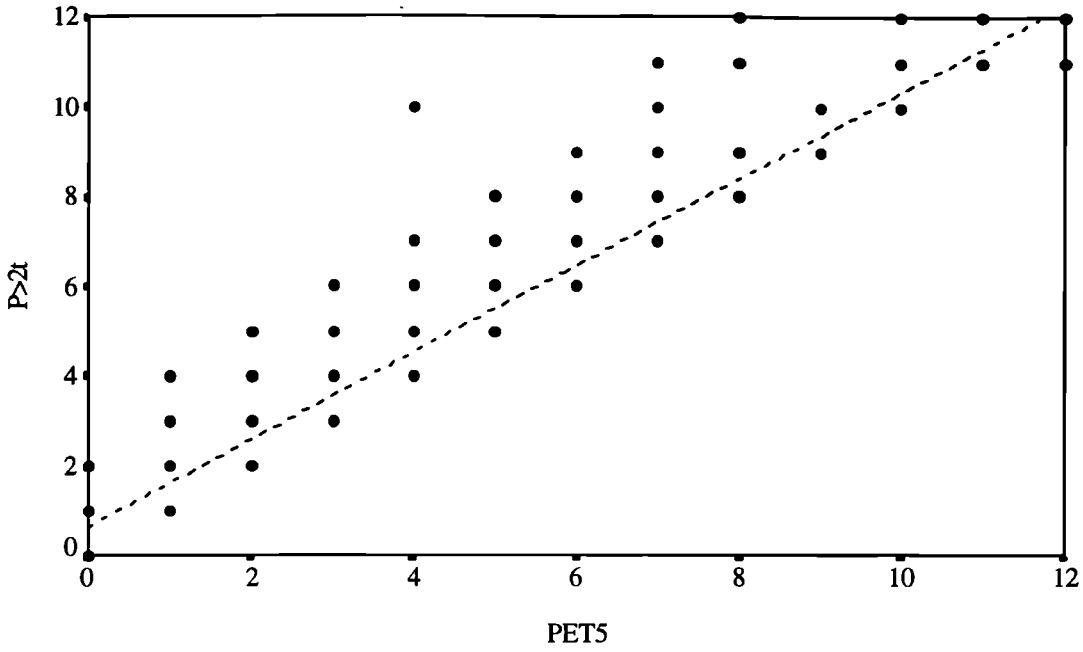


Figure 2.6.c. P>2t against PET5.

P>2t = 0.65 + 0.97 (PET5). (r^2 = .97; F = 5967.52; df = 1, 393; p = 0.00)

2.4.3. Wernstedt (1972) database

A series of indices of habitat productivity have been investigated. The aim of this investigation was to search for climatic indices as a proxy for habitat productivity. Further support for the use of the rainfall diversity index DIV and the index P>2t, was found from climate data sampled from Wernstedt (1972). The database consisted of 218 weather stations, sampled randomly across sub-Saharan Africa. The sample was a stratified sample, with data equally distributed among the vegetation zones of Africa described in Keay (1959). Significant least squares regressions are shown in table 2.8. and figures 2.7 a to e.

Table 2.8. Significant least squares regression equations from climate data in Wernstedt (1972) (see figure 2.10 a to e), n = 218.

Multiple regression equation*	Figure 2.10	R^2	*F(df)*	*P*
P>2t = 10.59 - 0.89 (*Mo50*)	a	0.89	373.12 (1, 88)	0.00
P>2t = 11.43 - 0.73 (*Mo100*)	b	0.82	178.92 (1, 88)	0.00
DIV = 0.611 0.74 (*Mo50*)	c	0.70	206.65 (1, 213)	0.00
DIV = 0.67 - 0.42 (*Mo100*)	d	0.43	45.16 (1, 199)	0.00
DIV = 1.36 - 0.63 (*P>2t*)	e	0.67	72.09 (1, 88)	0.00

* *P>2t* = number of months where rainfall is greater than twice the mean annual temperature; *Mo50* = number of months <50mm rain; *Mo100* = number of months <100mm rain; *DIV* = rainfall diversity index.

Conclusion

The index P>2t was shown in figure 2.4.a to c, to be directly correlated with direct measures of plant productivity (evapotranspiration). In this database, monthly data was available, therefore Mo50, Mo100, DIV and Z could be calculated. None of the correlations with Z are shown, since Z has already been shown to be correlated with direct and indirect measures of productivity (see table 2.5). The correlations between DIV and Mo50 or Mo100 were discussed in section 2.4.1. (table 2.5; figure 2.5. e and f). This data provides further support for the use of the more easily calculated indices, DIV and P>2t as good measures of habitat productivity.

Figure 2.7. Significant least squares regression equations of climate data from Werndstedt (1972). Regressions against the rainfall diversity measure DIV, validate its use. n = 218 weather stations, randomly sampled from sub-saharan Africa.

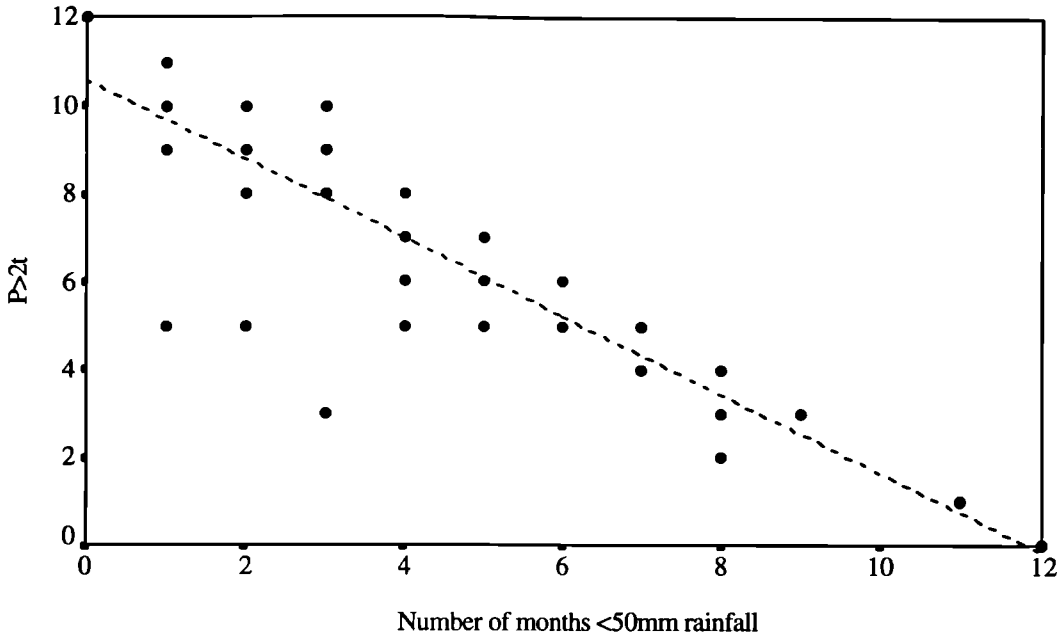


Figure 2.7.a. P>2t against number of months <50mm rainfall.
P>2t = 10.59 - 0.89 (MO50). (r^2 = 0.89; df = 1,88; F = 373.12; p = 0.00)

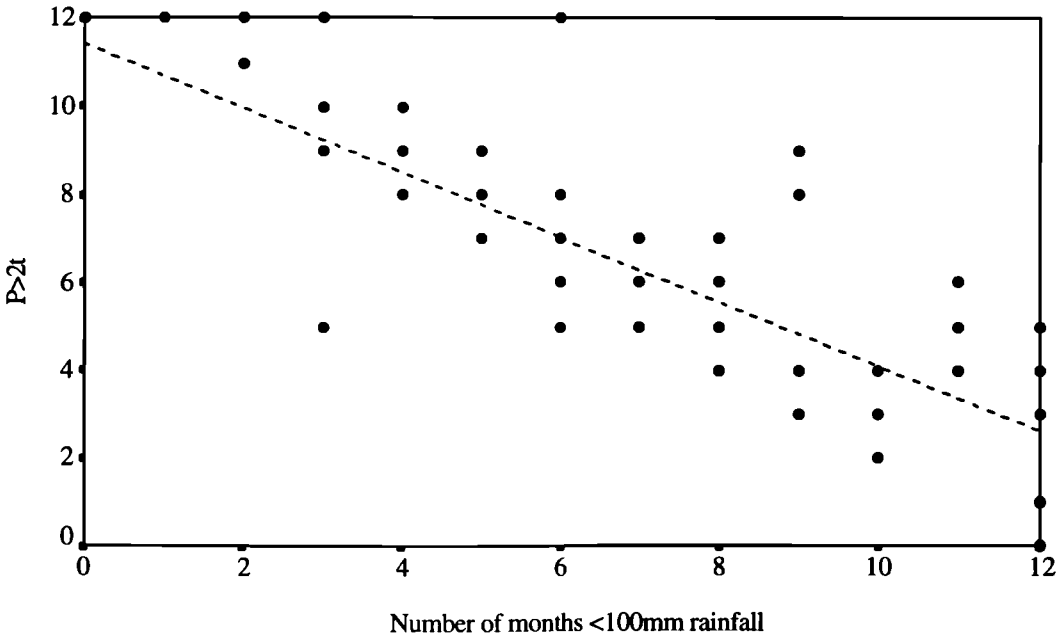


Figure 2.7.b. P>2t against number of months <100mm rainfall.
P>2t = 11.43 - 0.73 (MO100). (r^2 = 0.82; df = 1,88; F = 178.92; p = 0.00)

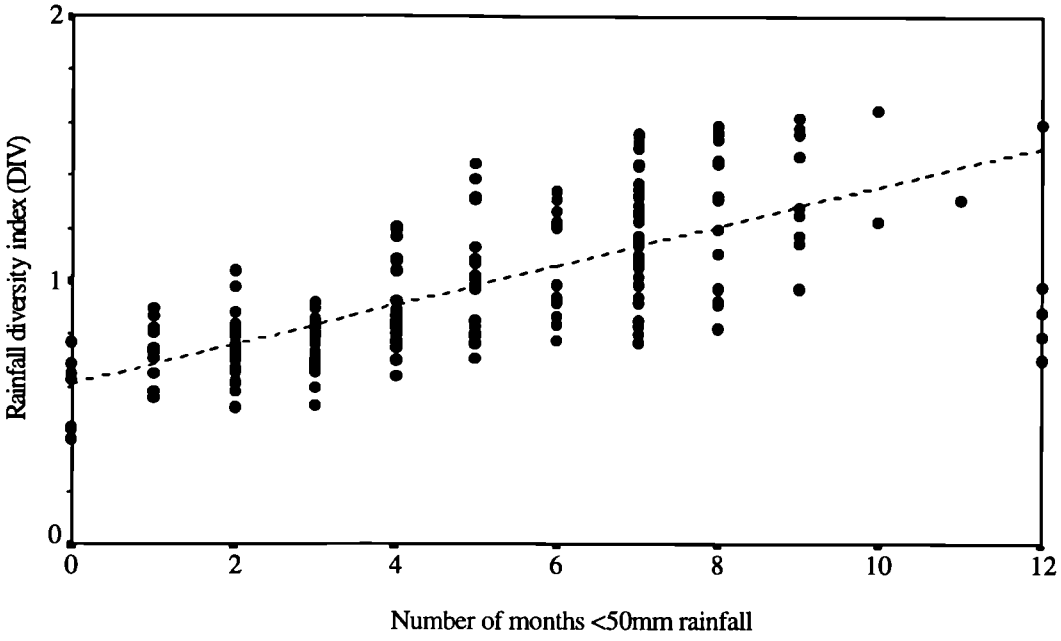


Figure 2.7.c. Rainfall diversity index (DIV) against number of months <50mm rainfall. DIV = 0.611 0.74 (MO50). (r^2 = 0.70; df = 1,213; F = 206.65; p = 0.00)

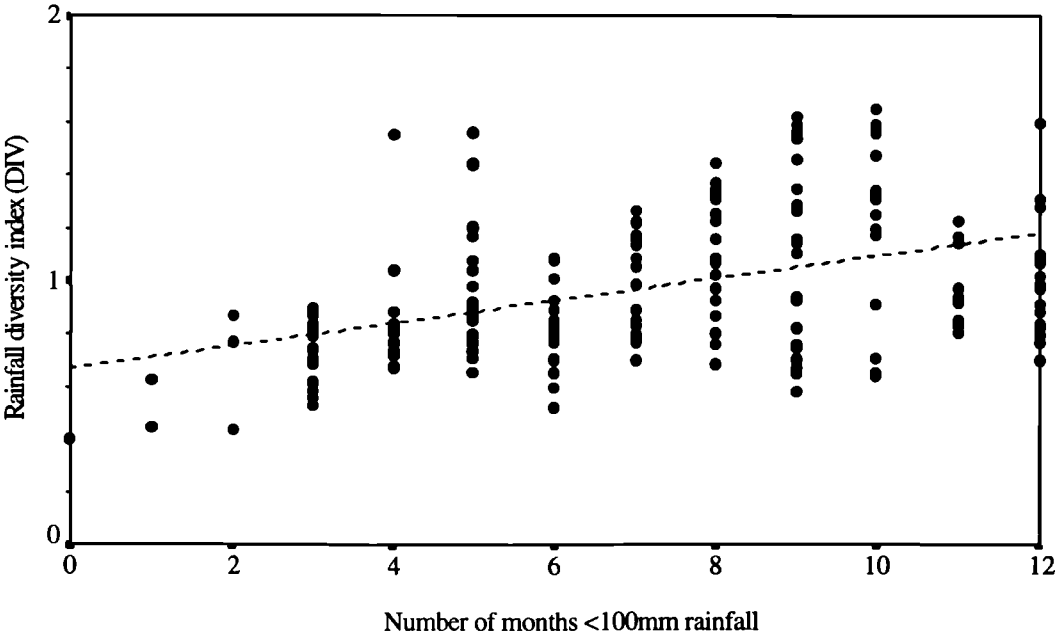


Figure 2.7.d. Rainfall diversity index against number of months <100mm rainfall. DIV = 0.67 - 0.42 (MO100). (r^2 = 0.43; df = 1,199; F = 45.16; p = 0.00)

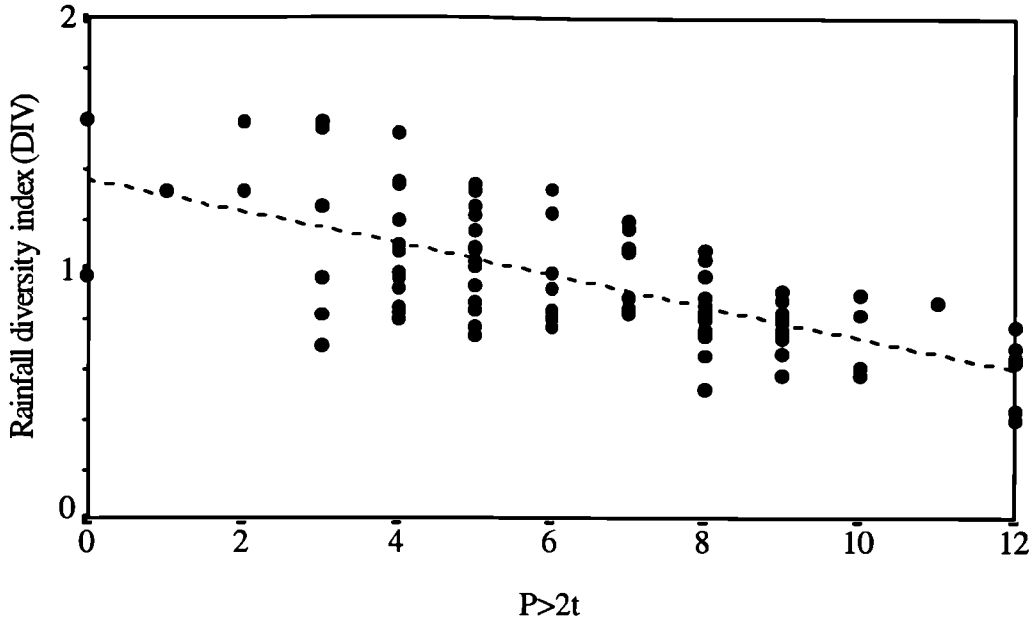


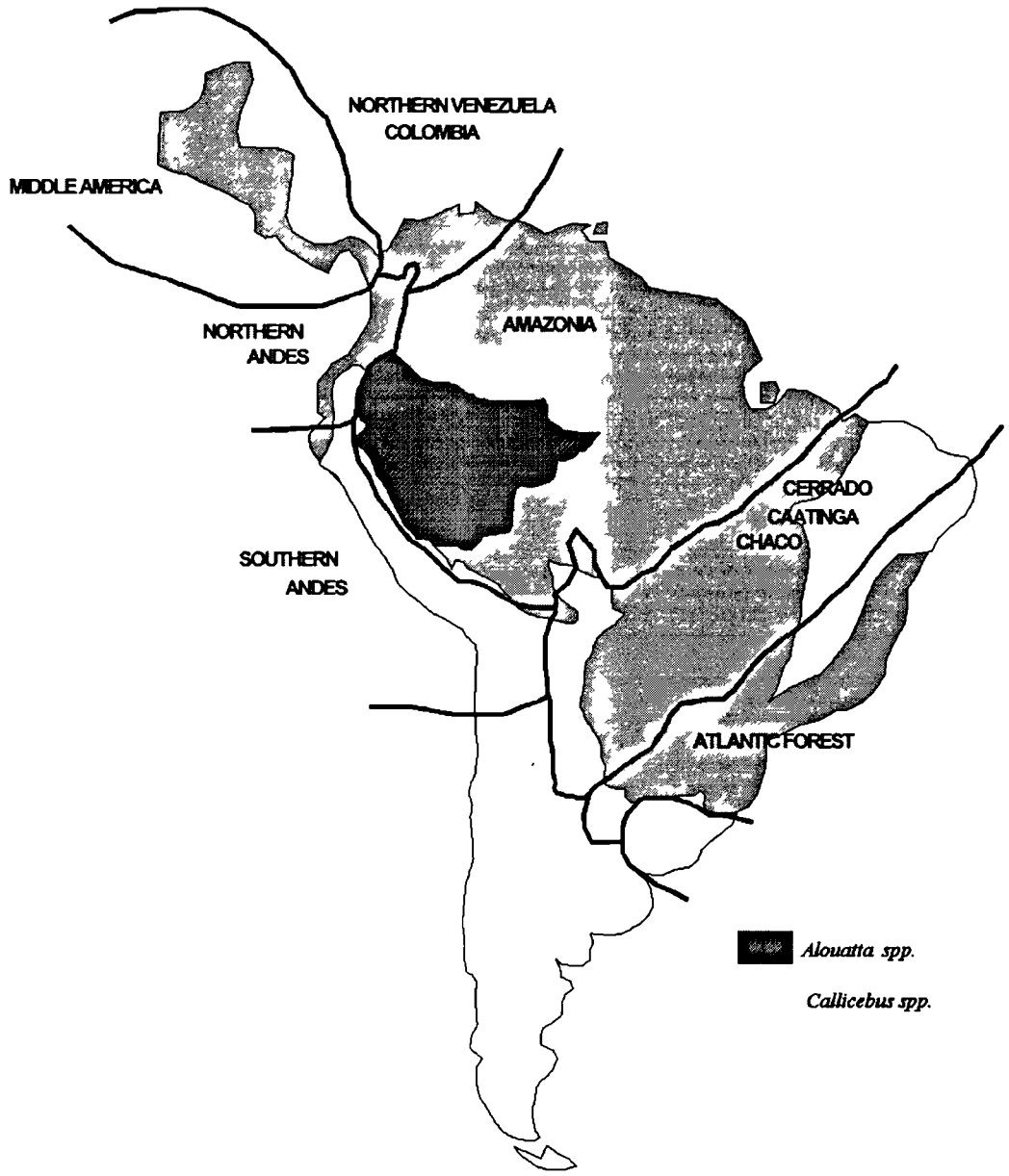
Figure 2.7.e. Rainfall diversity index (DIV) against P>2t
DIV = 1.36 - 0.63 (P>2t). ($r^2 = 0.67$; df = 1, 88; F = 72.09; p = 0.00)

2.4.4. Testing climate indices on New World climate data

The climatic indices investigated thus far have been based upon, and tested on African climate data. In an investigation of the effects of seasonality on the geographic distribution of Neotropical primates (Pastor-Nieto & Williamson, *in review*), rainfall seasonality was found to have a differential effect on platyrrhine primate distribution, based on their body size. Figure 2.8. illustrates the geographic range of a large and small body size platyrrhine (*Alouatta* and *Cebuella* respectively).

The new world, in contrast to the old world (Southern and Middle America), may be divided into nine phytogeographic zones (Gentry 1982). These phytogeographic zones accurately describe Neotropical vegetation diversity. Rylands (1995) subtracted two zones; the Caribbean, because there are no primates, and secondly the Guyana sub-region, which is subsumed into the Amazonian zone, to form seven phytogeographic zones in South and Central America. In addition to recording climatic data from the seven phytogeographic zones, climate data was recorded from the regions of overlap between the zones. We characterised each of the phytogeographic regions in terms of climate, with a view to predicting habitat productivity, because there is strong evidence that insect abundance, and fruiting and leafing phenology is highly correlated with rainfall diversity (Wolda 1978; Poulin *et al.* 1992; Terborgh 1983). The climatic database consisted of 118 weather stations that were randomly sampled from South America, evenly distributed amongst the phytogeographic zones (see table 2.10). Climatic data for overlapping zones were means of those zones overlapping. Regions of overlap were considered because some platyrrhine primates inhabit more than one phytogeographic zone.

Figure 2.8. A map of the geographic range of a large body size platyrrhine, *Alouatta* spp., and a small body size platyrrhine, *Cebuella* spp. Overlaid are the seven phytogeographic zones defined in Gentry (1982).



Subsequent abbreviations:
Cerrado/Caatinga/Chaco = CCCH; Amazonia = AM; Southern Andes = SA; Middle America = MA; Northern Venezuela-Columbia = NVC; Northern Andes = NA; Atlantic Forest = AF.

Table 2.10. Table of climatic variables calculated from long term records from 118 randomly sampled weather stations (Wernstedt 1972) for each of the phytogeographic zones (adapted from Gentry 1982).

Phyto-geographic zone *	Climatic variables					
	T	P	DIV	Z	MO<50	P>2T
CCCH	21.45	1164.62	.74	.89	3.65	8.68
AM	25.08	2118.01	.71	.90	2.18	9.79
SA	23.46	1407.29	.81	.89	3.13	10.67
MA	25.73	2876.04	.82	.89	2.00	9.90
NVC	22.60	2198.11	.79	.90	2.55	9.36
NA	21.31	772.75	.91	.85	6.00	6.57
AF	21.21	1439.75	.79	.90	2.71	9.57
CCCH/AF	21.33	1302.18	.78	.90	3.18	9.12
CCCH/AM	23.26	1641.31	.74	.89	2.19	9.24
AF/AM	23.14	1778.88	.75	.90	2.45	9.68
AM/SA	23.18	1443.37	.81	.87	4.09	8.18
AM/NA	20.34	1444.83	.82	.89	3.71	9.90
AM/NVC	23.83	2158.08	.73	.90	2.36	9.58
NA/MA	23.51	1854.58	.87	.87	4.00	8.24
NA/NVC	21.95	1485.42	.87	.87	4.27	7.97
MA/NVC	24.16	2357.07	.89	.89	2.27	9.63

*CCCH = Cerrado/Caatinga/Chaco; AM = Amazonia; SA = Southern Andes; MA = Middle America; NVC = Northern Venezuela-Colombia; NA = Northern Andes; AF = Atlantic forest.

** T = mean annual temperature; P = mean annual precipitation (°C); DIV = rainfall diversity index; Z=Simpsons index of diversity; Mo<50 = number of months where mean rainfall is greater is greater than 50mm; P>2T = number of months where rainfall (mm) is greater than two times the temperature (°C).

Rainfall seasonality (DIV), hence habitat productivity was shown to have and effect on platyrrhine body weight. None of the other indices of rainfall seasonality in table 2.10 had a significant relationship with platyrrhine body weight. The coefficient of variation in body weight, calculated from genus mean weights (see table 2.9) was correlated quadratically to habitat productivity (indexed by DIV). Variation in body weight decreases as seasonality increases, a narrow range of body weights are maintainable in more seasonal habitats. These results can be interpreted in the r- K-selection continuum (MacArthur & Wilson 1967). r-selected species, are subject to high density dependent mortality, conditions of unpredictable fluctuations in climate and food availability promote r-selection. The smallest body weight category plotted against DIV (fig. 2.10), has the most highly significant regression slope of all the body weight categories ($r^2 = 0.87$, $p = 0.001$). This result corresponds to "Kay's threshold" (Kay 1975, 1984), and applies to the whole order Primates. Smaller animals require a higher

protein content in their diet, therefore have a higher basal metabolic rate (BMR) and consequently higher energetic needs (reviewed in Ford & Davis 1992).

To illustrate that the indices tested on African climate data were also successful in predicting productivity in the New World, correlations were computed between indices computed from 118 weather stations from data in Wernstedt (1972) (see figure 2.11 a to f). Significant least squares regression equations are given in table 2.11.

Table 2.11. Significant least squares regression equations from New World climate data in Wernstedt (1972) (see figure 2.11 a to f).

Multiple regression equation*	Figure 2.11	R^2	*F(df)*	*P*
$Z = 0.92 - 0.01$ (*Mo50*)	a	0.74	138.4 (1, 115)	0.00
$P>2t = -43.47 + 59.09$ (*Z*)	b	0.75	145.22 (1, 113)	0.00
$P>2t = -0.99 + 12.06$ (*Mo50*)	c	0.96	1524.28 (1, 113)	0.00
$DIV = 0.54 + 0.08$ (*Mo50*)	d	0.84	270.65 (1, 113)	0.00
$DIV = 6.44 - 6.36$ (*Z*)	e	0.84	268.5 (1, 113)	0.00
$DIV = 1.53 - 0.08$ (*P>2t*)	f	0.85	286.24 (1, 113)	0.00

* *Z* = Simpson's index of rainfall diversity; *P>2t* = number of months where rainfall is twice the mean annual temperature; *Mo50* = number of months with <50mm rain; *DIV* = index of rainfall diversity.

Conclusion

The same relationships hold for the New World, as for the Old World (Africa), the rainfall diversity indices seem equally applicable to the New World. Only indirect correlations with productivity were made in table 2.9, without direct reference to direct measures of productivity such as evapotranspiration.

Figure 2.9. The relationship between platyrrhine body weight and rainfall diversity, indexed by DIV (DIV re-named RDV in Pastor-Nieto & Williamson *submitted*) for Southern and Central America (from Pastor-Nieto & Williamson, *submitted*).

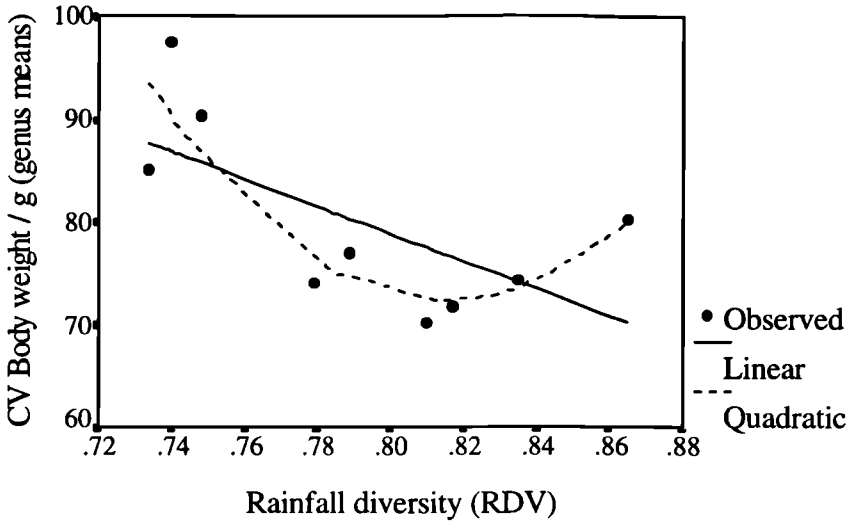


Table 2.9. Mean body weights for each of the platyrrhine genera.

Genus	Mean weight / grams
Alouatta	6500.92
Aotus	942.75
Ateles	7820.75
Brachyteles	10787.5
Cacajao	3165
Callicebus	1086.58
Callimico	585
Callithrix	279.88
Cebuella	128
Cebus	2704
Chiropotes	2807.5
Lagothrix	7042.5
Leontopithecus	585.17

Figure 2.10. The smallest platyrrhine species' body weight in each of the phytogeographic zones regressed against rainfall diversity (DIV).

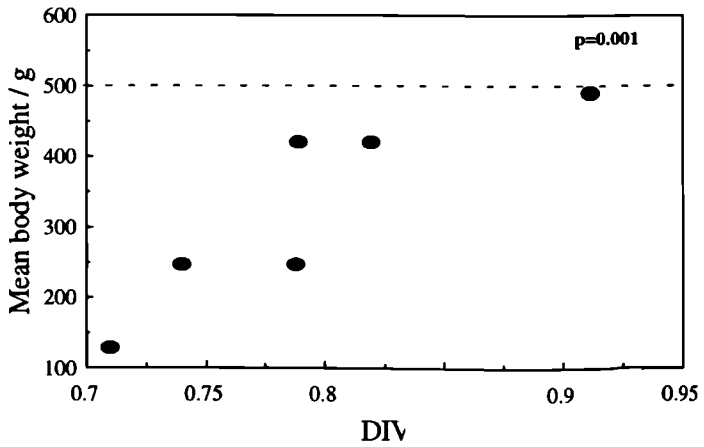


Figure 2.11. Significant regressions between climatic variables of Southern and Central America to illustrate that the same seasonality indices define habitat type and plant productivity in the New World as the Old World. Climate data from Wernstedt (1972), n = 118.

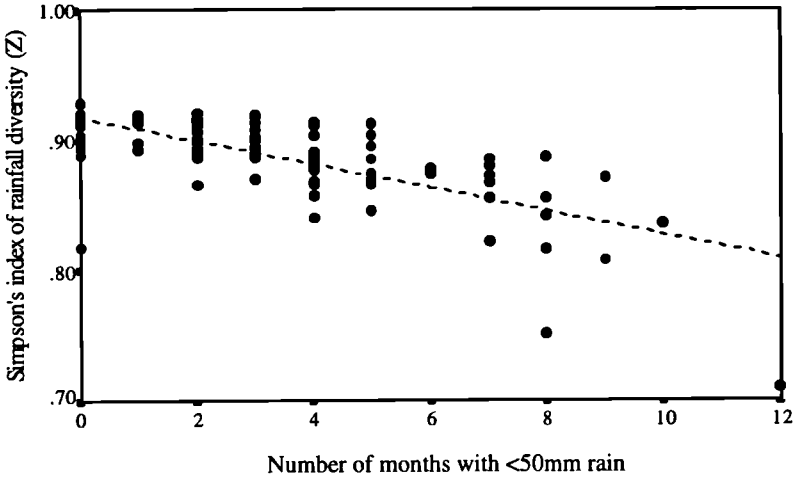


Figure 2.11.a. Rainfall diversity against number of dry months
Z = 0.92 - 0.01 (MO50). (r^2 = 0.74; df = 1, 115; F = 138.44; p = 0.00)

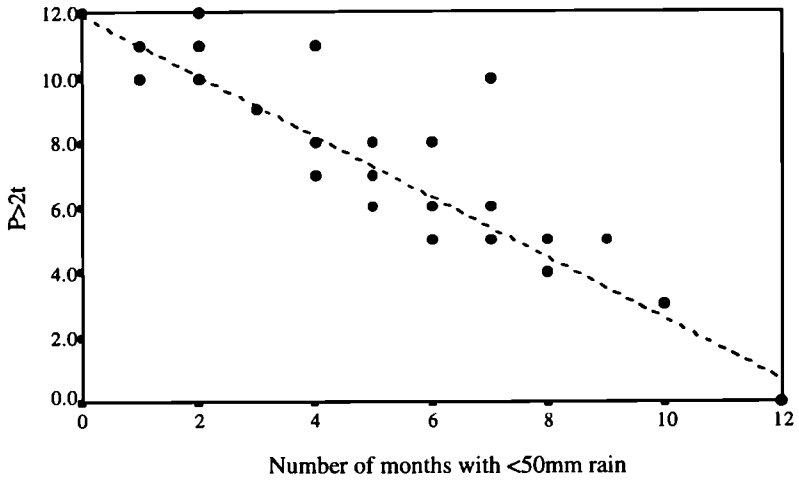


Figure 2.11.b. P>2t against number of dry months.
P>2t = -0.99 + 12.06 (MO50). (r^2 = 0.96; df = 1, 113; F = 1524.28; p = 0.00)

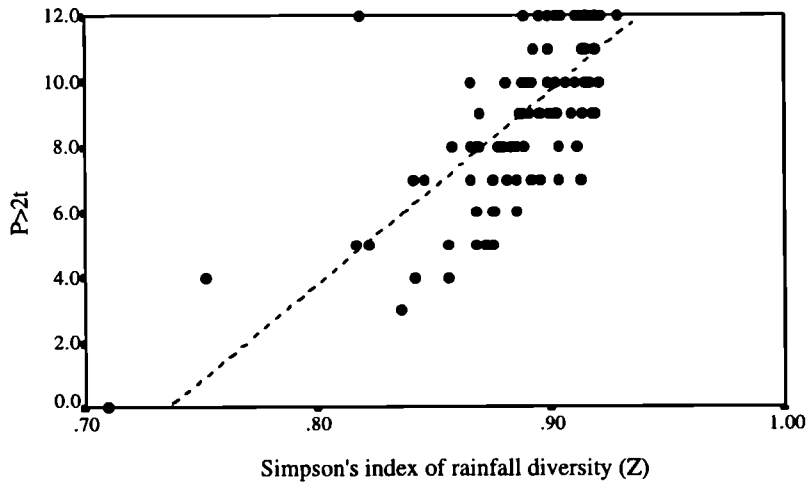


Figure 2.11. c. P>2t against rainfall diversity.
P>2t = -43.47 + 59.09 (Z). (r^2 = 0.75; df = 1, 113; F = 145.22; p = 0.00)

Figure 2.11. (Continued).

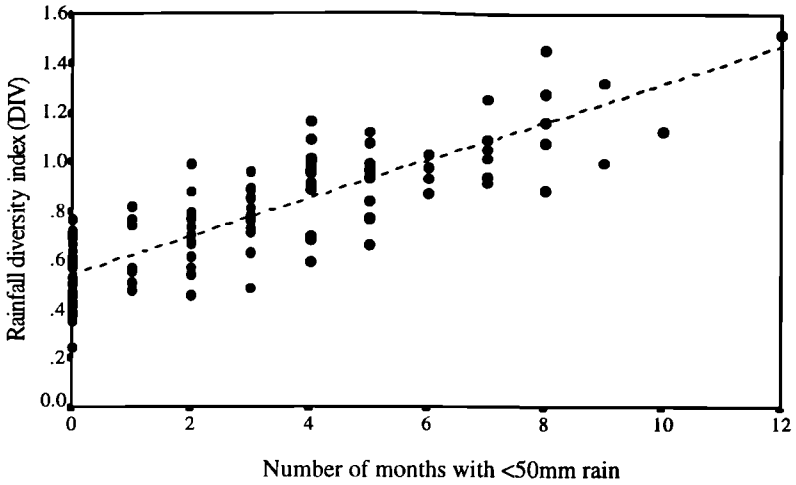


Figure 2.11.d. Rainfall diversity against number of dry months
DIV = 0.54 + 0.08 (MO50). (r^2 = 0.84; df = 1, 115; F = 270.65; p = 0.00)

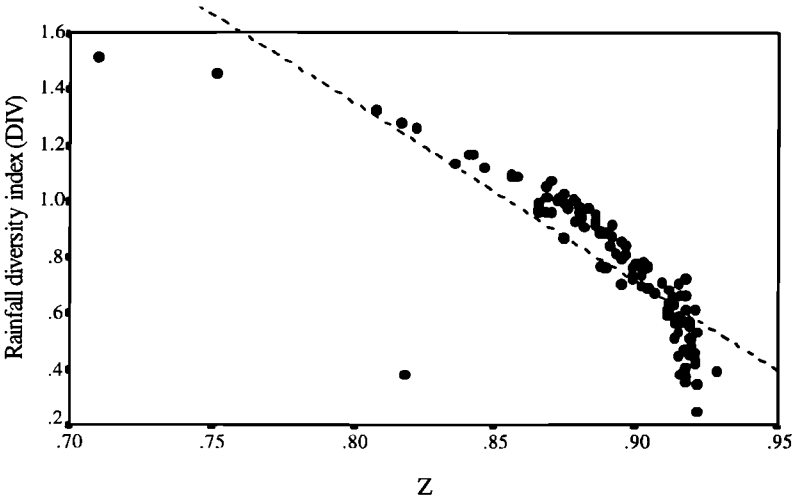


Figure 2.11.e. Rainfall diversity (DIV) against rainfall diversity (Z).
DIV = 6.44 - 6.36 (Z). (r^2 = 0.84; df = 1, 115; F = 268.5; p = 0.00)

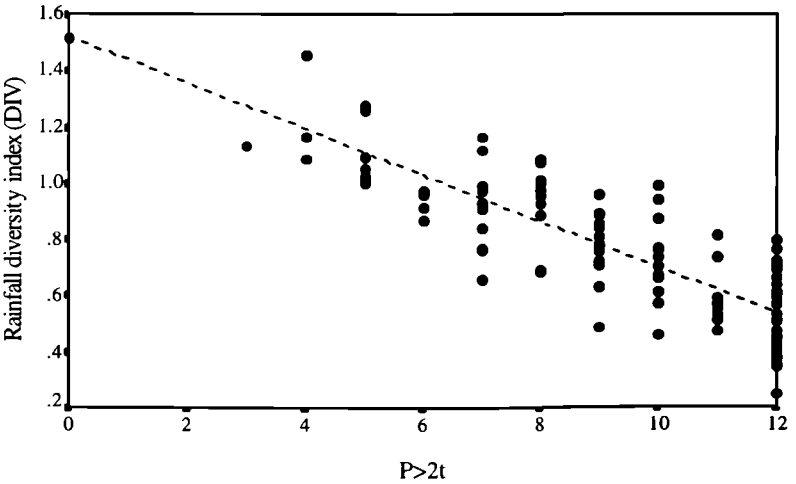


Figure 2.11.f. Rainfall diversity against P>2t.
DIV = 1.53 - 0.08 (P>2t). (r^2 = 0.85; df = 1, 113; F = 286.24; p = 0.00)

2.4.5. Reducing the number of independent climate variables

In the preceding sections, numerous climatic indices have been illustrated and tested. The purpose of these analyses were to identify simple indices to represent habitat productivity that could be used in systems models of primate socioecology. The statistical techniques used in these systems models (see chapter 2), of step-wise regression requires that the independent variables included do not co-vary. For example, in this chapter I have shown that many indices inter-correlate, all providing some measure of habitat productivity. A principal components analysis was conducted to investigate the minimum number of variables that could describe habitats based on climatic indicators (figure 2.12; table 2.12). This analysis suggests that the variance in the climatic indices can be explained in terms of three dimensions. Inspection of the way the indices are distributed in three-dimensional space suggests that these dimensions correspond to; some measure of rainfall, some measure of the temporal distribution of annual rainfall, and some measure of temperature. The reduction of climatic variables to three principal components will guide the selection of independent variables in step-wise regressions in chapters 2 and 3.

Figure 2.12. Principal components analysis of key environmental variables. Climate data from Wernstedt (1972), n = 218 randomly sample weather stations from sub-saharan Africa.

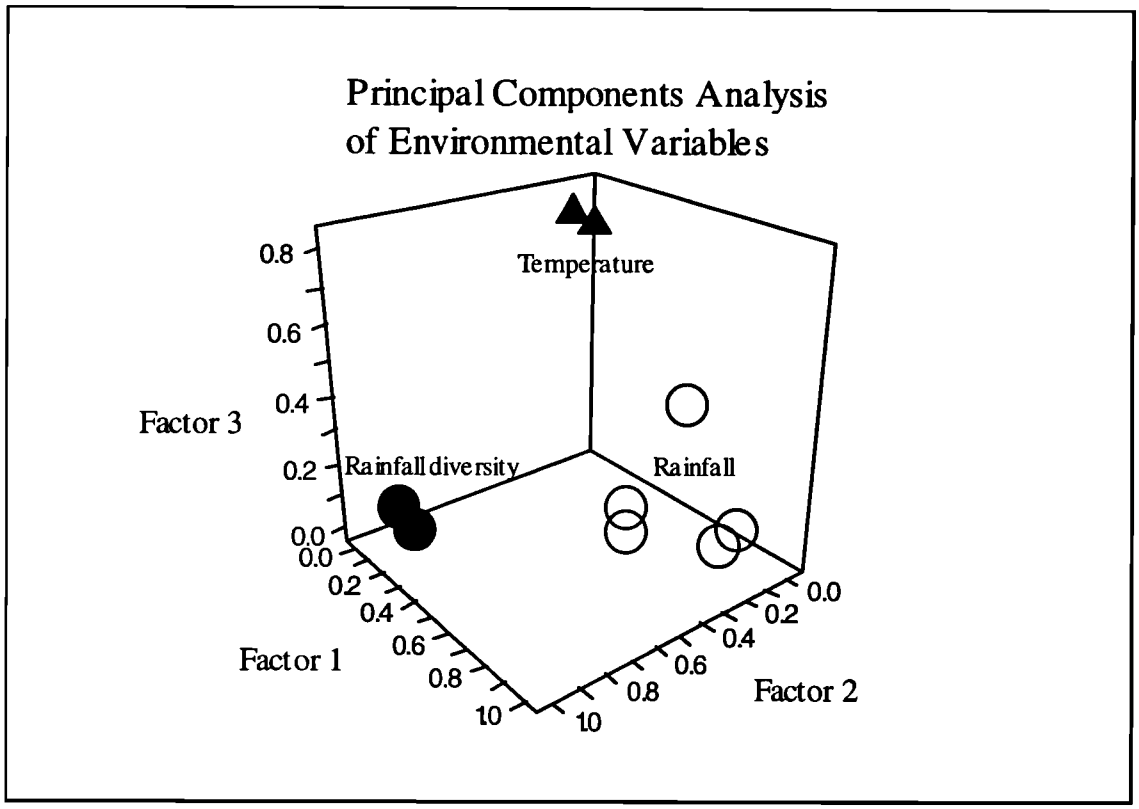


Table 2.12. Principal components analysis of environmental variables.

Variables*	Factor 1	Factor 2	Factor 3
LAT	*0.551*	-0.006	0.316
P	*-0.884*	-0.070	-0.062
Mo50	*0.901*	0.512	-0.163
Mo100	*0.927*	0.206	-0.071
P>2t	*-0.800*	-0.510	0.232
DIV	0.241	*0.951*	0.084
Z	-0.139	*-0.954*	0.113
ALT	-0.092	-0.042	*0.748*
T	-0.098	0.147	*-0.792*
Eigenvalue	4.431	1.683	1.014
% Variance	49.20	18.70	11.30
Cumulative % Variance	49.20	67.90	79.2

* LAT = latitude; P = rainfall / mm; Mo50 = number of months <50mm rain; Mo100 = number of months <100mm rain; P>2t = number of months where rainfall is greater than twice the mean annual temperature; DIV = rainfall diversity index; Z = Simpson's index of rainfall evenness; ALT = altitude / m; T = Temperature / C.

2.4.6. Constraints on Simpson's index of rainfall diversity

Rainfall seasonality (measured by Mo50 and Z) was found to have a significant effect on baboon time-budgets, and therefore maximum ecologically tolerable group sizes (Dunbar 1996). In a given temperature or rainfall regime, baboons were found to survive better in more seasonal habitats. As will be illustrated in chapter three, baboon maximum group sizes are simulated in two dimensions; rainfall and temperature. Consequently, any other climatic variables, beside temperature and rainfall, that are correlated with behavioural variables must be quantifiably related to temperature and rainfall. For example, the Wernstedt (1972) database showed that both the number of dry months (Mo50) and rainfall diversity (Z) were weakly related to rainfall (P) and temperature (T), as shown in the following equations.

$$Mo50 = 11.49 - 0.0078(P) + 1.5\times10^{-}6(P)^2 \qquad (r^2 = 0.714)$$
$$Z = 1.04 - 0.0122(Mo50) - 0.003(T) \qquad (r^2 = 0.475)$$

Since *Mo50* is related to P it was necessary to first define constraints on the possible range of values for *Mo50*. Table 2.13 shows the minimum and maximum rainfall values for each value of *Mo50*.

Table 2.13. Analysis of rainfall / number of dry months (*Mo50*) relationship, to determine a threshold rainfall for each value of *Mo50* (1-12). Climate data from Wernstedt (1972), n = 218.

Mo50	Mean rainfall /mm	Minimum rainfall / mm	Maximum rainfall /mm	Sample size (n)
0	2350.661	1512.32	3598.16	7
1	2183.038	1465.83	3396.99	12
2	1929.078	985.77	4159.76	27
3	1506.317	818.13	2824.73	32
4	1490.418	826.77	3228.59	25
5	1366.567	646.94	3776.22	22
6	1163.812	567.94	1758.44	15
7	783.641	431.54	1344.4	40
8	600.091	363.22	890.02	17
9	472.304	308.36	620.27	10
10	393.825	361.95	425.70	2
11	228.090	228.09	228.09	1
12	113.18	226.82	226.82	5

Quadratic and linear regression equations were computed for $Mo50_{mean}$, $Mo50_{max}$, and $Mo50_{min}$ (see figures 2.13 and table 2.14).

Table 2.14. Regression equations for the relationship between ecological variables. Climate data from Wernstedt (1972), n = 218.

Linear equation	Quadratic equation
$Mo50_{mean} = 8.166 - 0.0025(P)$ $r^2 = 0.51$, df = 1, 213, F = 219.75, p = 0.0	$Mo50_{mean} = 11.4897 - 0.0078(P) + 1.5E\text{-}06(P)^2$ $r^2 = 0.71$, df = 212, F = 265, p = 0.0
$Mo50_{min} = 10.316 - 0.0016(P)$ $r^2 = 0.47$, df = 10, F = 8.92, p = 0.014	$Mo50_{min} = 13.0646 - 0.006(P) + 1.2E\text{-}06(P)^2$ $r^2 = 0.67$, df = 9, F = 9.18, p = 0.007
$Mo50_{max} = 11.319 - 0.0073(P)$ $r^2 = 0.916$, df = 10, F = 106.97	$Mo50_{max} = 12.854 - 0.131(P) + 3.6E\text{-}06(P)^2$ $r^2 = 0.96$, df = 9, F = 109.97

With these equations the constraints on *Mo50* were defined and could therefore be used in the models of baboon socioecology presented in Dunbar (1996). These equations will subsequently be referred to in chapter 4, in the development of a model of chimpanzee socioecology.

2.5. CONCLUSION

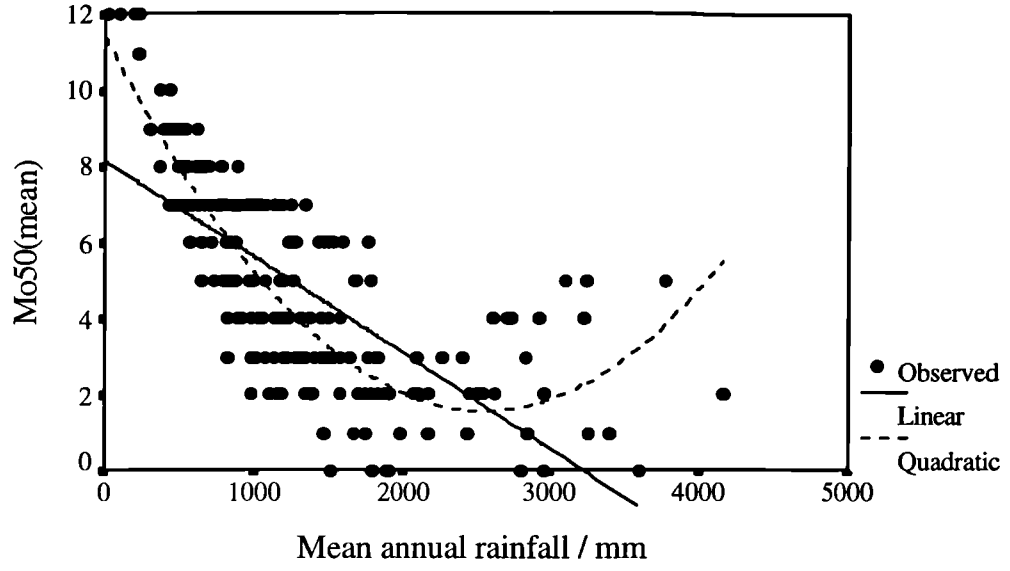
The aim of this chapter was to investigate a range of alternate meteorological predictors of plant productivity and habitat type. These indices will be used in subsequent chapters in the development of systems models of behavioural ecology, in which behaviour is correlated with environmental variables.

Indices were sought to define plant productivity from widely available climatic data. Indirect indices of productivity, using simple climatic measures, such as rainfall and temperature, were used as a proxy for direct measures of productivity, plant evapotranspiration. Data to compute evapotranspiration (e.g. wind speed, surface soil evaporation, hours of sunlight) were not available for either primate field site records, nor widely available from nearby weather stations. In addition to productivity, indices of seasonality; the temporal distribution of rainfall, were investigated.

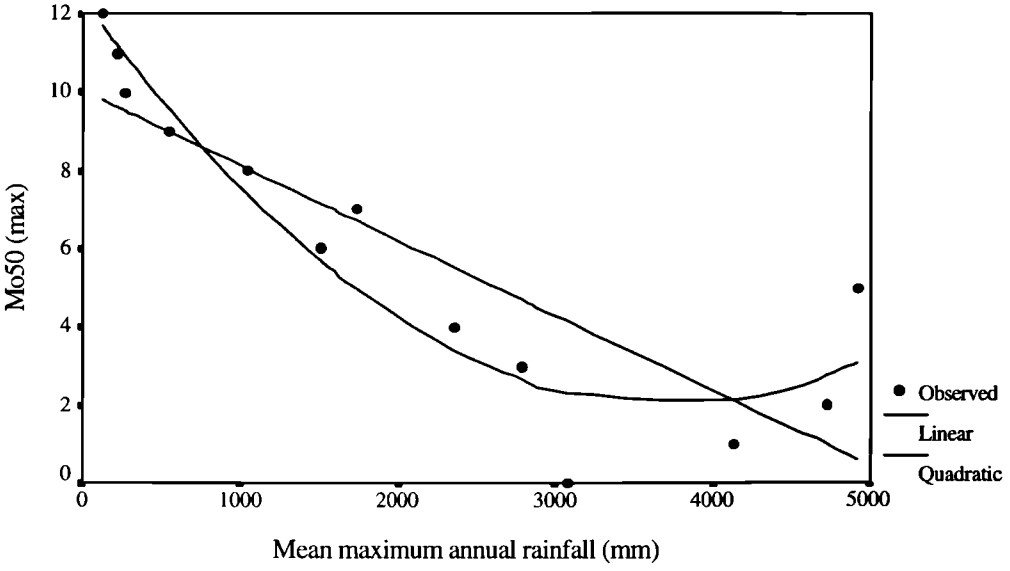
Definitions of seasonality and associated indices were reviewed. The seasonality index (SI) and seasonality ratio (SR) (see table 2.1) were concerned with seasonal contrasts. Absolute seasonality was indexed by defining the number of 'biologically dry months' when plants were in their dormant non-growing phase (P>2t; the number of months with less than 50mm rain, or 100mm rain).

Figure 2.13. Analysis of the relationship between number of dry months (Mo50) and rainfall, to determine a threshold rainfall value for each value of MO50 (1-12). Climate data from Wernstedt (1972).

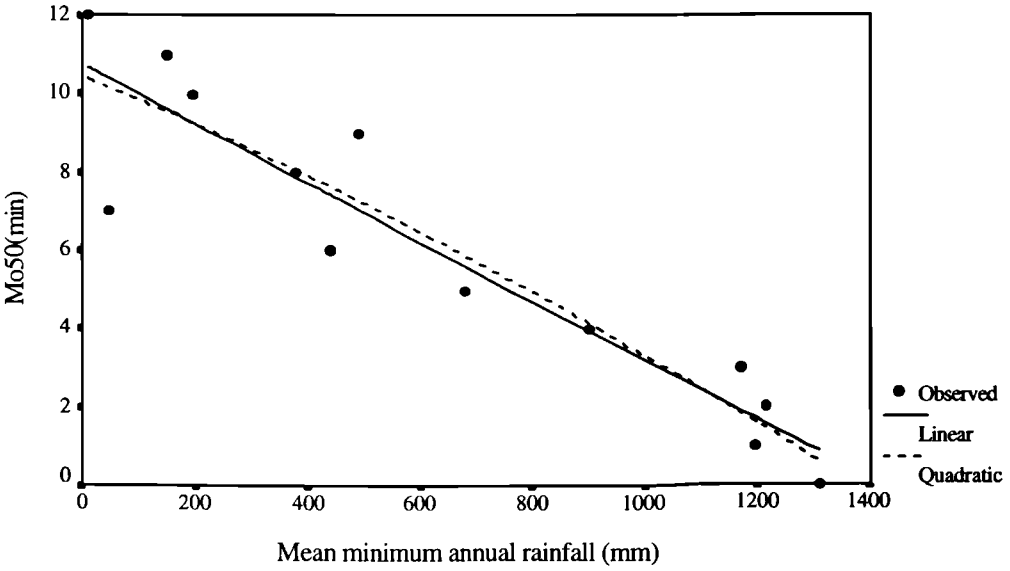
(a)



(b)



(c)



A new rainfall diversity index (DIV) was calculated, in the light of criticisms by Bronikowski & Webb (1996). An index of rainfall seasonality was sought that would be applicable to a range of rainfall regimes and magnitudes. The DIV index was easy to calculate, and showed the modality of rainfall, as illustrated with uni- and bi-modal rainfall distribution datasets (figures 2.2 & 2.3).

Diversity indices from the species diversity literature were used to characterise rainfall evenness, the spread of rainfall across the months of the year. Ideally for behavioural studies, we would choose an index based on how well it correlated with either an animal's behaviourally critical physiological state (direct effect of climate on the animal), or how well it correlated with the availability of resources of the animal in question (indirect effect of rainfall). If behavioural activity is affected by fluctuations in rain (mediated through changes in vegetation cover), the relationship between activity and rainfall variability should be robust to the choice from well defined variance measures. However, in search of a general index potentially applicable to a wide range of habitats, the indices were tested against a series of simulated rainfall regimes (table 2.3; fig. 2.4.a. & b.). The Shannon index of rainfall evenness had a good spread of values across a range of rainfall regimes. The Simpson (Z) index also had a good spread of values across rainfall regimes, however, there were defined limits to its maximum and minimum value which should be born in mind. Of the two indices not from the species diversity literature (SI and DIV), DIV had the widest range of values. A limiting factor with the use of DIV as an index was its high dependency on the actual rainfall values (as with the McIntosh index).

In addition to testing the indices on simulated rainfall regimes, databases of direct and indirect measures of productivity were used to further test the indices. The Thornthwaite & Mather (1962) database established that indirect measures of rainfall evenness, and hence productivity (DIV, Z, Mo50, Mo100) were highly correlated with direct measures of productivity (water deficit and annual evapotranspiration). The le Houérou & Popov (1981) database established that the P>2t index was highly correlated with direct measures of productivity (potential evapotranspiration). The great

advantage with the P>2t index is its ease of calculation from widely available data. The Wernstedt (1972) database showed that all the indirect measures of productivity (Mo50, Mo100 and DIV) were highly correlated with P>2t, which in the le Houérou & Popov database related to annual evapotranspiration. Therefore all the indirect measures were related to direct measures of productivity. The relationship between climate and plant productivity was exploited in an analysis predicting edible plant richness in southern Africa (O'Brien 1988). Minimum monthly potential evapotranspiration (*PEMIN*) and maximum monthly precipitation (*PMAX*), together explain more than 83% of the variance in plant species richness (*SppDiv*) (*SppDiv* = -61.28 + 2.98 (*PEMIN*) + 0.42 (*PMAX*); r^2 = 0.83; F = 138.12; SD = 19.97; n = 60; p = 0.0001) (O'Brien 1988). Species diversity was defined as the number of edible plant species per unit area. This analysis suggested that it might be possible to characterise the distribution of edible plants from a simple analysis of the relationship between plant type, seasonality and plant abundance (Peters *et al.* 1984). Satellite imaging of spectral information from plants has been shown to be sufficient to quantify productivity (e.g. Chong *et al* 1993), and to differentiate habitat types (e.g. Davenport & Nicholson 1993) in Africa. The conclusions from the analyses on climate station data in this chapter are sufficient to describe productivity, in the absence of access to more detailed satellite imaged data.

Having verified these results on African climates, the indices were tested on New World (central and south America) climate data. The south American data was useful in two ways. Firstly, the indices were not tested against direct measures of productivity; however the same relationships held between the variables. Further, the index DIV successfully differentiated the seven main phytogeographic zones of central and south America. The second purpose of the south American data was to illustrate the applicability of the DIV index in a behavioural study. Because the DIV index differentiated between habitat types, the body weight of small (<500g) platyrrhine primates was significantly related to DIV.

A large number of climatic variables, and rainfall indices were available from the meteorological literature. The aim of the chapter was to define variables for use in

regression models of behavioural ecology. Underlying assumptions of regression models require that there is sufficient variance in the independent variables, and the independent variables used were independent from one another and not inter-correlated. A principle components analysis of the variables examined revealed three key dimensions; some measure of rainfall, temperature and rainfall variability. This reduced the number of potential variables to three for use in subsequent chapters.

Recently, direct measures of potential evapotranspiration have been used to predict species richness in North America (Kerr & Packer 1997). The assumption of the analysis was that high energy availability in the habitat provides a wider resource base, permitting more species to coexist. Therefore it would appear that the indirect measures of potential evapotranspiration presented in this chapter could be applied to wider questions concerning species diversity.

The final analysis defined the constraints on the Simpson's index of diversity, a specific calculation used in an existing model of baboon socioecology (Dunbar 1996), and in this thesis.

Much of this chapter has focused on seasonality. Seasonality emerges as important variable in Human evolution (Foley 1991). Human evolution coincides with a marked increase in seasonal variation, and hence may be an important selection pressure. Geographically, widespread climatic shifts result in the migration of species as well as lineage turnover across clades and regions (Vrba 1985, 1988; Vrba *et al.* 1995). Recent focus of the relationship between climate and hominid evolution has been on temperature changes, which has been criticised (Sikes & Wood 1996; Vrba 1994). However rainfall seasonality, indexing predictability in the availability of resources emerges as an important factor (Wesselman 1995).

The analyses presented in this chapter emphasise the importance of rainfall seasonality for characterising habitat productivity. If we are to extrapolate the consequences of these seasonal definitions from their effect on extant animals to extinct species, caution should be exercised. Attributing features of contemporary ecosystems to prehistoric ones on the basis of a few similarities has been criticised (Lawrence 1971).

Actualistic studies of a range of southern and eastern African ecosystems (Peters & McGuire 1981; Peters *et al.* 1984; Peters & Blumenschine 1993) provide potential "frames of reference" for the interpretation of archaeological sites. Peters & Blumenschine (1995) compared modern wet and dry seasons at Olduvai to make inferences on past habitats; however, present day conditions can not be directly transferred to palaeoenvironments (Kappelman 1984; Plummer & Bishop 1994).

CHAPTER 3. BABOON SOCIOECOLOGY

CHAPTER 3. BABOON SOCIOECOLOGY

3.1. INTRODUCTION

In this chapter I shall review hypotheses for the importance of group size, and modelling techniques to predict group sizes in different habitats. The analyses in this chapter focus on the systems models (summarised in figure 1.1; section 1.2.1) of behavioural ecology. Primates use a suite of interrelated responses to ecological variability that include, changes in time budgets, shifts in home range, changes in the length of the active period, and changes in group size through fissions. The systems models presented in this chapter quantitatively examine variations in group size that are a consequence of optimisation decisions by the animals. Group size is a consequence of optimisation decisions about the optimal group size for a specific habitat. The costs and benefits of grouping are a function of local habitat conditions. Therefore the principal aim of the models is to examine quantitatively the relationship between environmental and demographic variables. The models are not concerned with the optimisation decisions themselves, but the *consequences* of those decisions. The functional relationships between environmental and demographic variables will provide information on the systematic constraints that act on animals' strategic decisions. The initial key question in all the models presented in this chapter is to identify the determinants of group size. Once group size has been determined, the models can be extended. For example, well established relationships between group size and life-history variables allow us to predict the composition and reproductive characteristics of the group.

3.2. GROUP SIZE

3.2.1. Maximum ecologically tolerable group size.

An animals' ability to survive in a particular environment depends on its ability to solve the specific ecological constraints that characterise that habitat. One modifiable behavioural trait is group size. Group size may be important for two reasons. Firstly, the more animals there are performing a behaviour, the more occurrences there are of it.

For example, more threats and harassment tend to accumulate on the lowest ranking members of the group because there are more animals to harass them. Secondly, an animal only has a limited time to interact with other members of its group, therefore the social experiences of other group members will decline as group size increases. One consequence is that groups may become increasingly fragmented with increasing group size.

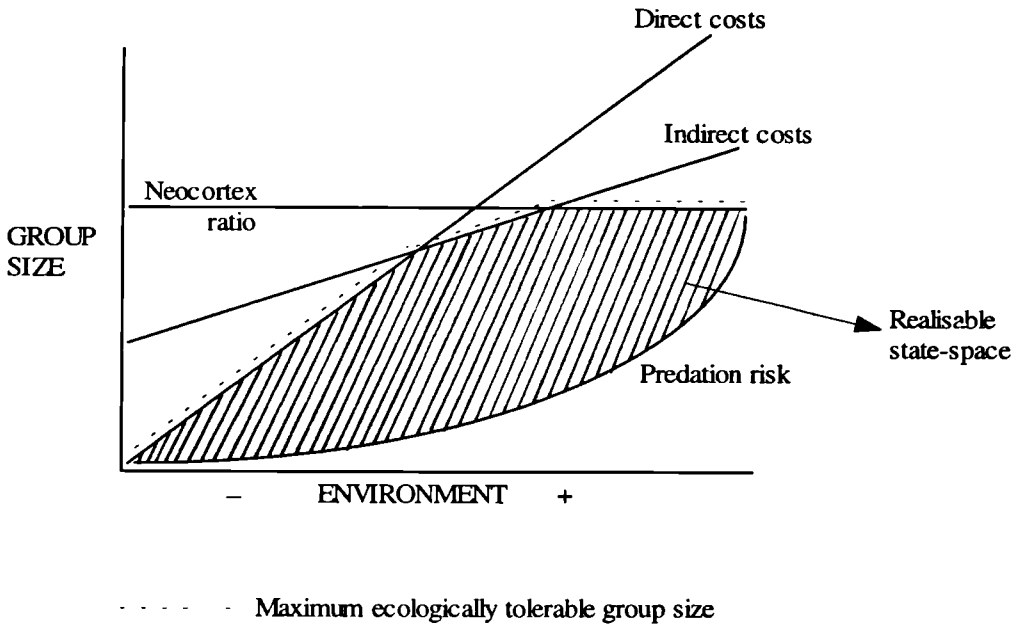
Group size is a trade-off between predation (favouring large groups) and the costs of too large groups, which give rise to social tensions. Grouping as an anti-predator strategy (Alexander 1974; van Schaik & van Hoof 1983; Terborgh 1983; Terborgh & Janson 1986) depends on the local density of predators and the availability of safe refuges, since it is predation *risk* that is important. Evidence suggests that predation risk is correlated with group size among forest living primates (van Schaik & van Noordwijk 1986), and is sufficient to explain differences in group size within communities.

Animal populations face a trade-off between gaining energy and avoiding predation (e.g. Houston *et al.* 1993). The trade-off between predation avoidance and the maximum socially cohesive group size gives rise to the optimum group size. The optimum group size will be habitat specific (Wittenberger 1980; Rutberg 1984; van Schaik & van Hoof 1983). Group size is limited by the availability and distribution of resources, which place an upper limit on group size. The maximum group size as illustrated by Dunbar (1988, fig. 7.5: 133) is a four-dimensional relationship. Individuals are trying to maximise their reproductive success, and group size is the behavioural response by which animals are able to meet this optimisation criterion (maximum reproductive success). In terms of optimality theory, the state variables are those variables which affect an animals' ability to reach the optimisation criterion, in this case habitat quality and predation risk. Therefore there is a four-dimensional relationship between group-size, reproductive success, habitat quality and predation risk.

An additional constraint on group size, is that of neocortex size (Dunbar 1992*c*). Group size co-varies with relative neocortical volume in non-human primates (Dunbar

1992*d*; Aiello & Dunbar 1993). The neocortex size seems to limit the number of social relationships an animal can keep track of. In evolutionary terms, neocortex volume has evolved in response to the environmental factors which constrain group size, and for this reason can be used as a predictor of group size. The neocortical constraint can be incorporated into the model of group size in the following schematic state-space diagram (adapted from Dunbar 1996; fig.1: 36).

Figure 3.1. State space diagram illustrating the maximum ecologically tolerable group size in primates.



This diagram is strictly schematic, the actual shape and magnitude of the lines serve only for illustrative purposes. The costs of group living are represented by the lines 'direct-' and 'indirect-costs'. Direct costs are those linked to resource dispersion and availability and the resulting feeding competition, which is a direct function of habitat quality. Indirect costs are the physiological stresses (reproductive suppression) of living close to others, physiological stress is a simple function of group size. Dunbar (1988) points out that these are average costs, since in some cases the costs are distributed unequally among the group members (for instance low-ranking individuals may bear a disproportionate portion of the costs). The costs of living in a group can differ between

the sexes, so that optimal dispersion patterns differ between the sexes (Wrangham 1979, 1982).

The 'realisable state-space' is the region of permissible group sizes, within which group size may be optimised to a specific value. The realisable state-space may be interpreted in terms of the formula for net reproductive rate $R_0 = \sum_x l_m m_x$. Where R_0 is an index of net reproductive rate, l_m is fecundity (subscript x indicates a specific period of time), m_x is survivorship (the proportion of individuals that survive from birth to age x). In the diagram 'predation minimisers' are those animals that maximise survival by minimising risk of predation, hence maximising m_x (survivorship) by living in the largest groups permitted in the realisable state space. 'Fecundity maximisers' are those animals that maximise the fecundity (l_m) side of the fitness equation. It is important to note that maximum ecologically tolerable group size is not the actual size of groups, but the limiting size that cannot be exceeded.

The maximum ecologically tolerable group size, derived from the time budget, can be used to predict the range of habitats the species in question could inhabit without showing signs of demographic stress (Dunbar 1992*b*). Given a species minimum time budget requirements, the range of habitats that meet those requirements, whilst maintaining groups of a habitat specific minimum size, can be investigated. Bronikowski & Altmann (1996) coined the phrase 'sky-down' modelling for models of baboon socioecology that seek to quantify the extent to which the behavioural ecology of socially living primates can be predicted from meteorological variables One of the most basic ecological questions that can be posed, is why organisms of a particular species are present in one area, but not in others. The limits on distribution are more complicated than "the environmental factor for which the organism has the narrowest range of adaptability or control" (Bartholemew 1958). Neither is a species distribution limited solely by its physiology. A constraints approach, similar in principle to the model followed in this thesis, is the theoretical framework adopted by Caughley *et al.* (1988) for defining the limits to species distributions. In the same way that the group size model considers constraints on individual fitness (predation risk, resource availability,

competition etc.), Caughley *et al.* (1988) define three constraints on ranging. Firstly an external factor that cannot be modified by the animal (e.g. temperature, rainfall, a specific substrate, or a source of non-depleting food or water). A second cost of ranging could be a depletable environmental factor, for example a consumptive resource, or a pre-emptively used resource. A consumptive resource, is a resource accessible to all group members, but its use reduces availability to others. A pre-emptively used resource, is a resource for which animals are winners or losers in obtaining it. A final constraint on ranging was suggested to be a deleterious environmental factor whose effect on an animal may vary with population density (e.g. parasites, pathogens or predators). The technique used by Caughley *et al.* (1988) specified the extent of range based on correlation, by trying to infer causality, and the nature of the limiting factors derived from the population (see Hoffman & Blows, 1994 for a review of evolutionary and ecological approaches to species borders).

So far I have only considered maximum group size. If the minimum group for survival is greater that the maximum ecologically tolerable group size, an animal will not be able to survive in that particular habitat (Dunbar 1996). The minimum permissible group size is assumed to be determined by the level of predation risk in a given habitat. Group size is a key behavioural means of deterring predators among primates (van Schaik 1983, Dunbar 1988). If minimum group size is to be determined, the effect of predation needs to be quantitatively examined. Because animals are responding to potential predation *risk*, simply measuring mortality does not index predation. The assumption underlying minimum group sizes is that animals adjust the minimum group size so that predation risk is equilibrated across different habitats (Dunbar 1996). Baboon predation risk my be positively related to the density of low level cover (ground and bush level cover), (Altmann & Altmann 1970; Byrne 1981; Rasmussen 1983; Dunbar 1989; Cowlishaw 1993), and negatively related to the density of large trees, which serve as refuges from predators.

Quantitative equations derived from nine east African sites of tree (*E*) and bush level (*B*) cover were used to predict minimum group size;

$\ln B = -2.072 + 1.811 \ln T$ ($r^2 = 0.36$)

$E = 86.26 - 14.078 Mo50$ ($r^2 = 0.85$)
(***B*** = bush cover; ***E*** = tree cover; ***T*** = mean annual temperature (°C); ***Mo50*** = number of months with <50mm rainfall).

Baboon minimum group size was predicted for the sample of baboon populations in Dunbar (1992*b*) giving the following best-fit equation (Dunbar 1996);

$\ln N_{min} = 2.67 - 0.23 \ln E + 0.202 \ln B$ ($r^2 = 0.516$, N=53, $p = 0.05$.

3.2.2. Other hypotheses for predicting maximum group size

van Schaik & van Noordwijk (1986) argue for risk of predation as a true independent variable in the complex equation predicting group size. Terborgh & Janson (1986) suggest that risk of predation is a constant function of group size, always decreasing with increasing group size regardless of species. In a given community of similar sized primates, risk of predation is a constant function of group size and inter-specific variation must depend on other extrinsic variables.

3.2.3. Variation in group size

Variation in group size is related to the stability of social groups, availability of food resources (Dittus 1977; Fedigan & Baxter 1984; Altmann *et al.* 1985; Caldecott 1986; Melnick & Pearl 1987), and competition for food between groups (Wrangham 1980; van Schaik & van Noordwijk 1986; Dittus 1987).

Beauchamp & Cabana (1990) investigated the effects of mean troop size, diet, territoriality and habitat upon temporal variability of group size in primates, using variance functions, relating mean group size and both within- and between-group competition.

3.2.4. Time budgets and group size.

Given an infinite amount of time, animals could always balance their nutrient and energetic budgets. Even in extremely poor nutrient habitats, given infinite feeding time, sufficient energy could be ingested (Southgate 1991). Nevertheless, time is limited, and there are competing demands on available time. Elements of the time budget compete, showing the importance of having time for non-subsistence activities ("free-time": Kiester & Slatkin 1974). Caraco (1979*a*, *b*) first considered the relationship between group size and time budgeting. In avian foraging flocks, overwinter survivorship depended on both energy acquisition rate (time allocation) and avoiding predation. Animals have a natural period of nutrient turnover, during this time their energetic demands must be met. Conventionally a 12 hour period is considered, mostly for ease of calculation, however this period may be altered. Therefore, animals are restricted by the amount of time available in which to schedule biologically essential activities. Time budgeting can be viewed as an optimisation problem, where carrying out an activity results in lost opportunities for another. Animals have to maximise benefit in the available time (McFarland 1974; Caraco 1979*a*,*b*; McFarland & Houston 1981).

Many ecological and social factors can affect time budgets. Time spent feeding can be influenced by body size, digestive physiology and diet quality (Janis 1976; Clutton-Brock & Harvey 1977). Primates feeding on poor quality food may increase (e.g. Nakagawa 1989) or decrease (Dasilva 1992) their feeding time. Time budgets are also affected by spatial and temporal availability in habitat quality and climate (Post 1981; Clutton-Brock *et al.* 1982; Iwamoto & Dunbar 1983). The nutritional demands of reproduction also influence the allocation of time (Altmann 1980, 1983). The duration of nursing in female baboons is constrained by the time needed to rest and socialise (Altmann 1980, 1983; Barrett *et al.* 1995; Kenyatta 1995). Finally, group size affects the allocation of time (Slatkin & Hausfater 1976; Caraco 1979*a*,*b*; Barnard 1980; Barnard *et al.* 1983; van Schaik *et al.* 1983).

The effects of one factor need not be universally the same. For example, in larger groups individuals may have to spend longer feeding because of increased competition

(baboons: Slatkin & Hausfater 1976; Stacey 1986; house sparrows: Barnard 1980; long-tailed macaques: van Schaik *et al.* 1983), or may feed more efficiently because their need for vigilance against predators is reduced (Juncos: Caraco 1979*a*,*b*; mixed-species flocks of shore birds: Barnard *et al.* 1983).

Often activities are taken out of feeding time (e.g. Waterbuck: Spinage (1968); Impala: Jarman & Jarman (1973); Feral horses: Duncan (1980); and Red deer: Clutton-Brock *et al.* (1982)). In these examples time is taken out of feeding for reproductive activities, rather than taking time out of resting time. Time budgets are also subject to digestive constraints. For example Giant Panda time budgets reflect the need of herbivores with the gut of a carnivore to conserve energy (Schaller *et al.* 1985).

There is a suggestion that it is foraging in association with males that limits scheduling of activities, and imposes a nutritional burden that limits female gregariousness and make it impossible in the case of orang-utans. The food-supply of gorillas (*Gorilla gorilla*) varies less in time and space than that of other great apes (Watts 1988), and will therefore affect the distribution of time budgets in gorillas.

A failure to consider social behaviour as part of a larger time allocation problem may well underestimate the costs that social interactions can represent in group living (Andrews & Rosenblum 1988).

3.3. PREVIOUS MODELS OF BABOON SOCIOECOLOGY

The original time-constraints approach to modelling the maximum ecologically tolerable group size of baboons (Dunbar 1992*b*) has subsequently been extended (baboons: Dunbar 1992*e*, 1994, 1996; Bronikowski & Altmann 1996: gelada baboons: Dunbar 1992*a*; gibbons: Sear 1994; hanuman langurs: Strivastava & Dunbar 1996).

The comparative socioecology models consider five species of baboon (*Papio hamadryas*, *P. anubis*, *P. cynocephalus*, *P. papio* and *P. ursinus*). The problem of phylogenetic inertia in comparative analyses (see Harvey & Pagel 1991) is argued not to be relevant here (Dunbar 1992*b*). Time budgets are viewed not as species typical traits, but as adaptations to local habitat conditions, and are therefore habitat specific.

Furthermore, the five species of *Papio* baboons are often better considered as sub-species (e.g. Smuts *et al.* 1987). Data from blood proteins (Shotake *et al.* 1987) indicate little differentiation between the sub-species of *Papio*, and genetic distances (Kawamuto *et al.* 1982) suggest that there is little difference between the cercopithecoid primates as a whole compared to congeneric species in most other taxa.

By developing functional models of primate socioecological systems we can explore further the relationship between environmental and demographic parameters. Predictions can be made on the first causes of grouping from variables affecting variation in group size. Although these models rely on the optimisation criteria constraining group size (see fig. 3.1), they do not explore the optimisation decisions *per se*, but the *consequences* of those decisions. By understanding the functional consequences of decision making, we are in a position to understand the constraints that act upon individuals strategic choices. The problem of optimal group sizes is considered as a linear programming model. Linear programming is the mathematical technique used for searching for the optimal set of control variables, and maximises (or minimises) an objective, given the constraints of inequalities, which are also linear functions. As illustrated in figure 3.1, the region of possible group sizes lies above the line generated by the benefit equations, and below those generated by the constraint equations.

Stepwise regression is used to develop functional equations, seeking equations with the best predictive power. These equations are then entered into a computer program to iteratively determine the maximum ecologically tolerable group size, given the constraints of the models inputs, defined by stepwise regression equations of environmental and behavioural variables.

3.4. REANALYSES OF MODELS OF BABOON SOCIOECOLOGY

3.4.1. Introduction

I reanalysed baboon time budget and ecological data, in the light of recent criticisms of the original time budget model presented in Dunbar (1992*b*) made by Bronikowski & Altmann (1996). The latter criticisms were based upon the original Dunbar (1992*b*) time

budget model, although Dunbar (1994; 1996) has subsequently built upon and improved this initial model (see above). The revisions presented in this chapter use the same original dataset. With access to the original sources for these data, corrections were made to behavioural and climate data. The re-analysis is focused on the two main areas of criticism raised in Bronikowski & Altmann (1996) and Bronikowski & Webb (1996); data collection and statistical methods of analysis. Bronikowski & Altmann (1996) were not solely concerned with re-analysing Dunbar (1992*b*), but were concerned with the wider issue, as to whether a few climatic variables can accurately predict changes in resources and the adjustments in time budgets by populations to such changes.

3.4.2. Data

Two types of data are considered in these analyses; behavioural and ecological/environmental. The data are derived from 18 populations of baboons (genus *Papio*) from sub-Saharan Africa (see Dunbar 1992*b*; fig.1: 36 for a map of the sampled populations and data sources). These 18 populations form the core sample, most of whom have data on time budgets, group size and climatic variables. In addition, a further two subsidiary samples were detailed, with which to independently test the functional equations derived from the core 18 populations. Some of the same study sites appeared in the core and subsidiary samples, but were considered independent data points when data had been collated five years apart, *or* if there had been a significant demographic change in the study troop.

i. Environmental data

In the original analysis, Dunbar (1992*b*), used either single year, or average meteorological data for the baboon field sites considered. Study site data was used where possible, due to its greater accuracy in proximity. Where this was lacking, long-term average climatic data was used from nearby weather stations. This mixture of long and short term data may have been important. Since the climatic data was used to index plant productivity, a time lag would be expected between rainfall, and its effect on plant

productivity. Therefore long-term average rainfall may be a more accurate reflection of the constraints plant productivity places on the populations, than study year rainfall.

A second issue regarding climatic variables in the baboon socioecology models is the selection of variables. This issue was considered carefully in chapter 2, and will be considered further here, in particular the use of different rainfall diversity indices (see section 2.3).

ii. Behavioural data

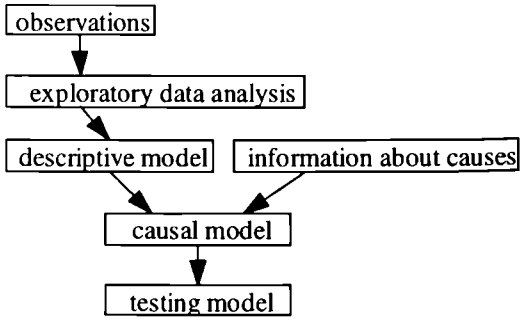
In addition to correcting time-data, misprinted in Dunbar (1992*b*), further data on Amboseli was presented in Bronikowski & Altmann (1996), which is included in these analyses.

3.4.2. Methods

i. Statistical methods

In order to determine the factors that influence baboon time budgets, stepwise multiple regression was used. This would find the set of environmental variables that accounted for the highest proportion of the observed variance in the time budget data.

The majority of statistical analyses in this and the subsequent chapters utilise multivariate statistics, specifically step-wise regression. Often sample sizes are relatively small where behavioural data on long-lived primates is concerned. Therefore, I shall consider here in detail the advantages and disadvantages of multivariate statistics. James & McCulloch (1985) suggest a hierarchical set of procedures in multivariate analysis research.



Multivariate statistics have the following objectives: To predict one variable from others, to investigate the association of an independent variables with a dependent variable in the presence of other variables. Finally, if causal models are appropriate (usually with experiments), to investigate cause and effect. Nevertheless there are limitations to multivariate statistics. Although multivariate statistics allow good predictability, they do *not* however allow inference of *causation.* Furthermore predictions should only be carried out in situations similar to those in which the model was derived.

Opinion is divided over the reliability of step-wise regression procedures. On the one hand Wilkinson (1987) refuses to include a stepwise regression program in a recent edition of the SYSTAT manual. Wilkinson (1987) does not accept that an automatic selection procedure can find; a) the best fitting model, b) the real model and c) alternative models. On the other hand, those that advocate step-wise regression procedures, do so with caution. Automatic selection procedures are useful in that they select a subset of the variables that do an *adequate* job of prediction (James & McCulloch 1990). The key issue in step-wise regression, is whether to rely on the automatic selection procedure of computer statistics packages, to select a sub-set of 'meaningful' variables. Most researchers reach a compromise, where selection variables are first combined into biologically meaningful groups. This step also excludes the possibility of violating the assumption of no collinearity of independent variables. Multiple regression is concerned with finding the "best" set of predictor variables. The best set of predictor variables is a combination of parsimony and adequacy of prediction.

The following guidelines were followed when constructing step-wise regression equations. Variables were first screened for violation of the assumptions of multiple regression; linearity, equality of variance, independence of error, normality and locating outliers. If any of the above assumptions were violated, the following options were considered. A non-linear variable may be transformed, for example logged for positively skewed data, square-root for negatively skewed data. Relevant to the data considered in

this chapter (time budget percentages), an arc sine transformation should be made to dependent variables that are in the form of proportions (as in a percentage) or a rate.

As mentioned above, a major assumption of regression analyses is that the data are normally distributed. Conventionally, log transformation is performed to normalise skewed data. However there are a number of transformations suitable for specific directions of skew, listed below

Data transformations for skewed data (see Tabachnik & Fidell 1989).

Distribution of data	Transformation
Moderate +ve skew	SQRT (X)
Substantial +ve skew	LOG (X)
Severe +ve skew	1 / (X)
Moderate -ve skew	SQRT (K - X), K = constant, largest score + 1
Substantial -ve skew	LOG (K-X)
Severe -ve skew	1 / K - X

Data in this chapter will be log transformed to maintain comparability with existing equations (also see Bronikowski & Altmann 1996).

The second stage is to construct the multiple regression model. A correlation matrix should be constructed for all variables, noting any large inter-correlations between independent variables (multicollinearity). In the statistics package, SPSS for windows, the statistic tolerance may be computed at each step to warn of multicollinearity. Introducing redundant variables in the same analysis reduces degrees of freedom for error, and weakens the analysis. Only when independent variables are uncorrelated (orthogonal) with each other are the tests of individual regression coefficients independent of one another. It is the correlation structure of the data base that guides the selection of variables.

The final stage is to build the model. Statistical packages provide three procedures for multiple regression; step-wise, forward and backward selection. In the forward method, variables are added to the equation one at a time. At each step the variables with the smallest probability of F is entered, provided it meets the *p*-value for inclusion (set by the programmer). Forward selection is the reverse of backwards selection. Stepwise selection begins with the current equation, then at each step it checks whether firstly any variable in the equation should be removed according to the *p*-

value for exclusion, or if any variable not already in the equation should be entered, according to the *p*-value for inclusion. Stepwise is a combination of forward and backward procedures. The first variable is selected in the same manner as forward selection. If the variable fails to meet entry requirements, the procedure terminates with no independent variables in the equation. If it passes the criterion, the second variable is selected based on the highest partial correlation. If it passes the entry criterion, it also enters the equation. From this point on variables are entered, and removed from the equation. To prevent the same variable from being repeatedly entered and removed, *p*-value to enter must be less than the *p*-value to remove. Variable selection terminates when no more variables meet entry and removal criteria.

Since the three procedures do not always result in the same equation it is often suggested that several acceptable models are developed and one chosen, based on interpretability and ease of variable acquisition. The stepwise method is often suggested as the best compromise between finding an optimal equation for predicting future randomly selected data sets from the same population, and finding an equation that predicts the maximum variance for the specific data set (Darlington 1990; Draper & Smith 1981). Sometimes important variables are left out, the addition or deletion of a variable can sometimes cause a complete change in the membership of the predictor set. However, it is important to always bear in mind that the purpose of stepwise multiple regression is to find the smallest set of predictor variables that still does an adequate job of prediction. Variables left out of the predictor set may be important, but omitted because they correlate with other variables in the predictor set.

Before accepting the results of a multiple regression equation, it is suggested that the results should be at least consistent with biological theory. The signs of the coefficients should be checked to see if they are reasonable, and make sense biologically. However, because the coefficients are partial regression coefficients, the sign of the coefficient can not be relied upon (Sokal & Rohlf 1984: 627). Partial regression coefficients may differ in sign and magnitude, depending on which independent variables are kept constant, although, within regression equations, the signs of independent

variables will still have the same relative signs to one another. The last, and final stage is to test the equations on independent sets of data. Due to the sensitivity of the multiple regression model, the original sample may not be representative of the population.

One final option, besides the stepwise, backwards and forwards selection criteria, is to build the model manually. This may be done by examining the F change between variables as they are added. The optimal number of independent variables is reached when the r-squared value no longer increases as independent variables are added. Nevertheless there are limits, and an equation with more variables does not necessarily provide a better fit to the data.

To summarise, the data must first be screened, then a suitable model selected, and finally careful interpretation of the multiple regression model made.

Bronikowski & Altmann (1996) used the statistical package Statview 4.01 for the Macintosh. To supplement this, PC SAS and Systat 5.2 for the Macintosh were used to verify the results. This precaution was taken in the light of correspondence, where we found the same data used in different statistical packages did not produce the same regression equations. It was concluded that the differences may be one or more of the following: (a) different algorithm for stepwise regression, or (b) some packages require F-value inclusion criteria, while others require a significance level inclusion criteria (*p*-value) or both. All the results presented here are conducted on SPSS 6.0 for Windows. The SPSS default settings are FIN(3.84) and FOUT (2.71).

ii. Building the model systems model of baboon socioecology

In building step-wise multiple regression equations, a hierarchical causal order of independent variables was imposed. Time allocations to different activity categories are interrelated because the number of daytime hours is fixed. Therefore animals will trade time allocations to different categories against one another. Resting time is particularly flexible, in that it is a reserve of uncommitted time that can be converted into other activity categories when required (see Dunbar & Sharman 1984, Dunbar & Dunbar

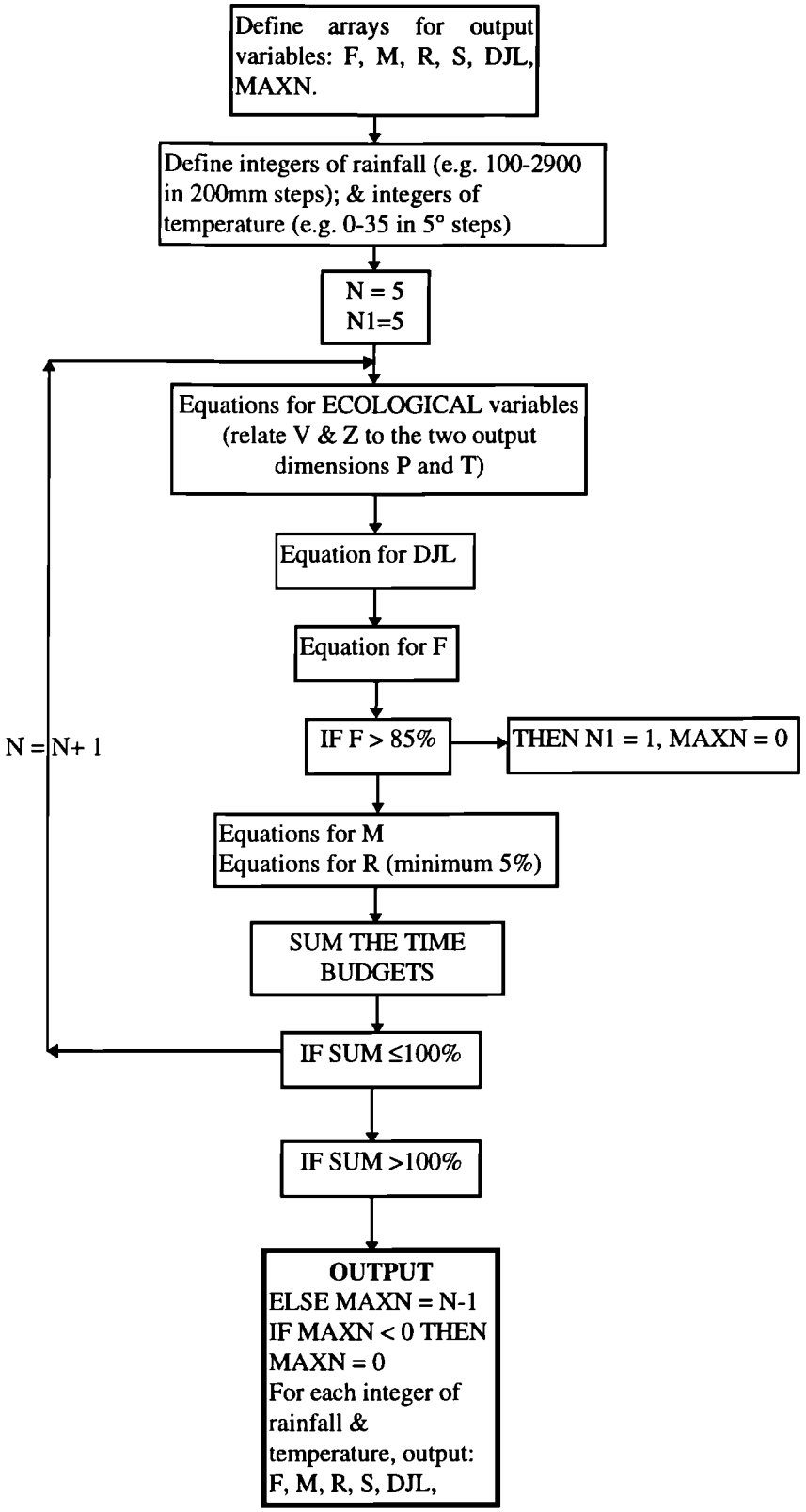
1988). The time budget data available reflect the allocation of time animals have given to different activity categories, given the particular constraints acting on those animals. If we want to determine how animals *ought* to devote time to activity categories in the absence of constraints, we have to make a series of assumptions. Dunbar (1992*b*) imposed a hierarchical order when constructing functional equations, to reflect biological priorities for the animals. Time spent feeding was assumed to be an absolute priority and independent of time spent in any other activity. Therefore for feeding time equations, all other time budget categories were excluded as dependent variables. Time spent feeding was assumed to be a possible determinant of time spent moving. No restrictions were placed on time spent resting or socialising.

Once functional equations had been derived, they were used as inputs for an iterative model, written in BASIC. The maximum ecologically tolerable group size for two dimensions; rainfall and temperature. For a particular rainfall and a particular temperature, the program determined, given the environmental constraints on each of the time budgets, whether an animal could sustain group sizes in that environment. If the time budgets could not be balanced in a particular temperature/rainfall regime, then a group size of zero was returned. The following flow diagram illustrates the sequences in the BASIC model.

The program first defines output arrays for each of the variables (feeding, moving, resting and social time, day journey length and maximum ecologically tolerable group size). Next, the integers of rainfall and temperature for which maximum ecologically tolerable group size will be predicted, are defined. Multiple regression equations relating ecological variables are then defined, followed by equations for day journey length and feeding time. The order in which the equations are presented, depend on the predictor variables in the equation. For example, if feeding time enters the equation for resting time, the equation for defining feeding time should occur in the program above the equation for resting time. Constraints were place on feeding and resting time. Feeding time could not be greater than 85% of the total time budget. A minimum of 5% resting time was permissible. Five percent was assumed to be the

baseline resting time that would be required given the thermoregulatory constraints of the environment. The maximum ecologically tolerable group size is determined iteratively by increasing group size in each cycle of the model, and summing the time budgets. When the time budgets combined account for 100% of the available time, the program prints the maximum ecologically tolerable group size for each integer of rainfall and temperature in a table.

Figure 3.2. Flow diagram to illustrate the BASIC model to predict maximum ecologically tolerable group sizes.



Key: Multiple regression equations for: **F** (feeding time); **M** (moving time); **R** (resting time); **S** (social time); **DJL** (day journey length /km^2).
MAXN = maximum ecologically tolerable group size; **N** = group size.

3.4.4. Aims of reanalyses

To summarise, the aims of the reanalyses of the baboon socioecology models are as follows:

1. To investigate the effect of the proximity of climate data to the field site, and the time-scale of climate data used.
2. To include additional time budget data from Amboseli, and correct data from Dunbar (1992*b*).
3. To compare the multiple regression equations in Dunbar (1992*b*; 1996) with those obtained by Bronikowski & Altmann (1996) and this study.
4. To investigate the effect of different inclusion criteria of the regression model on the resultant equation.

3.5. RESULTS

3.5.1. Climate Data

To clarify further the source of the climate data presented in Dunbar (1992*b*), table 3.1. lists the sources of climate data by site. Table 3.2. details the proximity of long-term weather stations to the study site locations. In some cases proximity has been sacrificed at the expense of obtaining long term data, in particular Giants Castle (South Africa) and Chololo (Kenya). The accuracy of Altitude is also important, since temperature is directly correlated with altitude (see principal components analysis: fig. 2.12). The advantage of weather station data, is the availability of a wider variety of climate measures, as seen in table 3.3. Study year climate data were obtained from the primate literature, and where possible from accurately placed weather stations near to the baboon field studies. These climatic compilations were government publications for the country concerned, housed at the Meteorological Library, Bracknell, Berks, UK. Summary data for the duration of study at each field is given in table 3.4, and listed in full in table 3.5.

Time budget data corrected from Dunbar (1992*b*) are listed in table 3.6. Corrections were made to Chololo time budgets, and more recent time budget data for

Amboseli (Bronikowski & Altmann 1996) added to the database. The final climatic data used was a mixture of long and short term climate data, this time emphasising proximity to the study site (table 3.7). With access to the original check sheets, I was able to correct errors made in the climate data (table 3.8). The subsidiary tables referred to in table 3.8 correspond to those in table 2 (Dunbar 1992*b*), the subset of data used to independently test the equations derived from the main sample.

Table 3.1. Climate data corrected from Dunbar (1992). Data listed for study years only.

Site	Reference	Map Reference
Awash	Monthly Weather Report Addis Ababa. Imperial Ethiopian Government Ministry of Communications. Civil Aviation Administration Meteorological Department. Weather station: Awash. Mean of 1971, 1972, 1973 values.	8°50' 40°09'
Bole	As above. Weather Station: Addis Ababa. Mean of 1971, 1972, 1973 values.	9°00'N 38°44'E
Mulu	As above	9°00'N 38°44'E
Gombe	Temperature from McGrew *et al.* (1981). Rainfall and rainy days read off graph in Goodall (1986). Years 1973, 1974, 1975, 1978.	
Amboseli	Data from Bronikowski & Altmann (1996)	
Mikumi	Data from Anon (1984).	
Cape	South Africa Monthly Weather Review. Weather Station: Cape Town. Mean of years 1975 - 1980.	33°58'S 18°36'E
Assirik	Data from McGrew *et al.* (1981). Mean of years 1976-1979	
Giants Castle	South Africa Monthly Weather Review. Weather Station: Cape Town. Mean of years 1975-1980.	33°58'S 18°36'E
Gilgil	Kekopey long term records (Dunbar pers comm.). Mean of years 1969-1980.	
Budongo	Data from Aldridge-Blake (1972; cited in Dunbar 1992*b*) PhD. thesis	
Ruaha	Dunbar (*pers comm.*).	
Chololo	Data from Barton (1986) PhD. thesis.	

Table 3.2. Table of long-term data sample locations (from Anon 1984), compared with study site locations.

Site	Source	Map reference	Altitude /m
Mount Assirik	*Study*	12°53'N 12°46'W	150
	HMSO	13°46'N 13°41'W	44
Bole Valley	*Study*	09°25'N 38°50'E	1700
	HMSO	09°02'N 34°45'E	2408
Awash Falls	*Study*	09°25'N 38°50'E	2300
	HMSO	09°02'N 34°45'E	2408
Budongo	*Study*	01°45'N 31°28'E	1015
	HMSO	01°41'N 31°43'E	1146
Chololo	*Study*	00°16'N 36°32'E	1600-1700
	HMSO	00°01'N 37°00'E	1937
Gilgil	*Study*	00°30'S 36°30'E	2000(east) 1768 (west)
	HMSO	00°31'N 35°00'E	2073
Amboseli	*Study*	02°40'S 37°10'E	1127
	HMSO	02°19'N 37°59'E	1339
Gombe	*Study*	05°00'S 29°30'E	680 (lake shore)
	HMSO	04°53'S 29°38'E	885
Ruaha	*Study*	07°23'S 36°31'E	1230
	HMSO	07°40'S 35°45'E	1428
Mikumi	*Study*	07°15'S 37°10'E	550
	HMSO	07°15'S 37°10'E	579
Giants Castle	*Study*	29°00'S 29°00'E	1953
	HMSO	33°56'S 18°29'E	12
Cape Hope	*Study*	34°15'S 18°25'E	50
	HMSO	33°56'S 18°29'E	12

Table 3.3. Climate data from an H.M.S.O. compilation (Anon 1984). Weather stations nearest to the baboon field sites were selected.

	Temperature / °C								Relative Humidity / %		Rainfall / mm			Number of months with rainfall					
	Daily			Monthly			Absolute												
Site	max	min	mean	max	min	mean	max	min	05:00am	11:00pm	mean	Total	days	<50mm	<100mm	DIV	Z	P>2t	Altitude /m
Assirik	35.5	20.8	28.15	43.7	9.6	26.65	45.2	6.9	69	41	55.0	915	160	7	8	1.35	.776	5	44
Bole	22.7	8.1	15.40	28.0	-1.4	13.30	29.6	-4.0	84	48	66.0	1115	79	5	8	1.07	.849	7	2408
Mulu	22.7	8.1	15.40	28.0	-1.4	13.30	29.6	-4.0	84	48	66.0	1115	79	5	8	1.07	.849	7	2408
Awash	32.9	17.7	25.30	39.4	8.1	23.75	40.0	0.0	71	41	56.0	610	92	9	10	1.05	.851	4	900
Budongo	28.5	16.7	22.60	34.1	13.4	23.75	36.9	12.0	81	56	68.5	1319	93	2	3	0.81	.904	10	1146
Chololo	23.6	8.6	16.10	27.7	2.8	15.25	27.3	0.7	71	52	61.5	760	61	9	11	1.02	.902	10	1937
Gilgil	23.8	9.3	16.55	28.5	4.1	16.30	30.6	1.66	73	47	60.0	1103	251	5	7	0.53	.888	12	2073
Amboseli	24.5	15.2	19.85	29.6	10.7	20.15	31.3	9.1	89	72	80.5	851	165	6	8	1.03	.838	7	1339
Gombe	27.9	19.1	23.50	33.1	14.6	23.85	36.8	13.2	76	65	80.5	962	107	6	6	0.91	.868	7	885
Ruaha	25.4	13.7	19.55	31.3	8.0	19.65	33.0	4.5	71	51	61.0	711	102	5	8	1.55	.821	5	1428
Mikumi	30.1	18.6	24.35	35.3	11.3	23.30	36.7	9.2	84	55	69.5	851	100	6	9	1.01	.863	6	579
Giants Castle	21.9	12.7	17.30	36.9	3.3	20.10	40.9	0.3	76	*	76.0	620	85	7	10	0.95	.880	6	12
Cape Hope	21.9	12.7	17.30	36.9	3.3	20.10	40.9	0.3	76	*	76.0	620	85	7	10	0.84	.880	6	12

* Missing data

Table 3.4. Table of climatic data, from study year sources (see table 3.2). Italicised columns used in staticstical analysis.

		Temperature / °C								*Relative humidity*			*Rainfall / mm*			*Number of months with rainfall*				
		Monthly			Daily			Absolute												*Altitude*
Site	Years data	*max*	*min*	*mean*	max	min	mean	max	min	*a.m.*	*p.m.*	*mean*	*total*	days	max	*<50mm*	*<100mm*	*P>2t*	*Z*	*/m*
Assirik	1971-3	*35.9*	*24.2*	*30.1*	*	*	*	*	*	*	*	*	*953.9*	84.3	*	*3*	*7*	*5*	*.817*	*150*
Bole	1971-3	*22.0*	*10.1*	*15.8*	*	*	15.7	*	*	*77.7*	*48.8*	*58.4*	*1043.0*	*	47.2	*6*	*5*	*7*	*.799*	*2354*
Mulu	1973-5	*22.0*	*10.1*	*15.8*	*	*	15.7	*	*	*77.7*	*48.8*	*58.4*	*1043.0*	*	47.2	*6*	*5*	*7*	*.799*	*2354*
Awash		*33.3*	*18.4*	*24.7*	*	*	24.4	*	*	*66.3*	*35.3*	*50.4*	*517.2*	*	41.8	*9*	*10*	*4*	*.858*	*400*
Budongo	1972	*28.3*	*14.1*	*22.0*	*	*	*	*	*	*	*	*	*1886.0*	*	*	*2*	*9*	*10*	*.886*	*1015*
Chololo	1982-4	*32.3*	*11.9*	*22.1*	*	*	*	*	*	*	*	*	*597.0*	*	*	*8*	*9*	*5*	*.846*	*1661*
Gilgil	1969-80	*25.5*	*10.6*	*17.3*	*	*	*	*	*	*	*	*	*729.8*	87.2	*	*4*	*11*	*11*	*.907*	*1768*
Amboseli		*31.9*	*14.2*	*23.1*	*	*	*	*	*	*	*	*	*225.0*	*	*	*11*	*	*	*.820*	*1127*
Gombe	1973-5	*28.0*	*19.0*	*23.5*	*	*	*	33.0	16.0	*	*	*	*1417.0*	151.5	*	*4*	*6*	*8*	*.861*	*680*
Ruaha		*	*	*21.7*	*	*	*	*	*	*	*	*	*304.0*	*	*	*3*	*1*	*3*	*.718*	*1230*
Mikumi	1946-61	*30.1*	*18.6*	*24.3*	35.3	11.3	24.1	36.7	9.2	*84.0*	*55.0*	*68.3*	*851.0*	100.0	112.0	*6*	*9*	*6*	*.863*	*579*
Giants Castle	1975-80	*22.7*	*12.8*	*16.5*	*	*	*	28.3	6.4	*82.1*	*57.2*	*69.8*	*483.3*	97.0	37.3	*8*	*12*	*6*	*.886*	*12*
Cape Hope	1975-80	*22.7*	*12.8*	*16.5*	*	*	*	28.3	6.4	*82.1*	*57.2*	*69.8*	*483.3*	97.0	37.3	*8*	*12*	*6*	*.886*	*12*

* missing data **Table 3.5**. Year by year climatic data for baboon sites.

Table 3.5. Year by year climatic data for baboon sites.

		Temperature (°C)								Relative humidity (%)			Rainfall (mm)			Months with rainfall <			Seasonality	
		monthly			daily			absolute										Altitude		
site	year	max	min	mean	max	min	mean	max	min	a.m.	p.m.	mean	total	days	max	50mm	100mm	(m)	p>2t	z
Awash	1971	31.7	17.0	*	*	*	23.5	*	*	69.0	38.0	55.1	752.2	*	49.6	9	10		3	.897
	1972	33.7	18.7	*	*	*	24.5	*	*	64.8	32.6	50.0	479.9	*	47.3	9	11	400	4	.829
	1973	34.5	19.5	*	*	*	25.3	*	*	65.0	36.0	46.0	319.5	*	28.5	9	12		3	.800
	mean	33.3	18.4	*	*	*	24.4	*	*	66.3	35.3	50.4	517.2	*	41.8	9	10		4	.858
Bole & Mulu	1971	21.5	10.1	*	*	*	15.5	*	*	80.6	50.0	62.0	1175.0	*	42.1	6	5		6	.818
	1972	21.8	10.4	*	*	*	16.1	*	*	80.0	51.0	58.0	837.0	*	25.0	6	5	2354	8	.817
	1973	22.7	9.7	*	*	*	15.4	*	*	72.5	45.3	55.3	1118.0	*	74.6	6	5		7	.761
	mean	22	10.1	*	*	*	15.7	*	*	77.7	48.8	58.4	1043.0	*	47.2	6	5		7	.799
Gombe	1973	*	*	*	*	*	*	*	*	*	*	*	1513.0	149.0	*	4	6		8	.841
	1974	*	*	*	*	*	*	*	*	*	*	*	1321.0	154.0	*	4	5	680	8	.867
	1975	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*			
	mean	28.0	19.0	*	*	*	*	33	16	*	*	*	1417.0	151.5	*	4	6		8	.861
Amboseli		31.9	14.2	*	*	*	*	*	*	*	*	*	225.0			11		1127		.820
Mikumi	1946-1961	30.1	18.6	*	35.3	11.3	24.1	36.7	9.2	84.0	55.0	68.3	851.0	100.0	112.0	6	9	579	6	.863
Cape &	1975	21.8	10.5	*	*	*	*	29.7	8.4	83.0	57.7	71.0	539.4	86.0	50.6	7	9		6	.810
Giants Castle	1976	21.5	12.0	*	*	*	*	28.2	6.2	83.4	59.0	71.0	587.4	119.0	43.5	8	11		8	.840
	1978	20.7	12.9	*	*	*	*	30.4	6.2	81.1	56.2	69.0	394.2	104.0	26.2	9	12		6	.894
	1979	21.3	12.4	*	*	*	*	25.2	5.5	80.9	55.6	68.0	407.3	77.0	28.1	9	12	12	6	.864
	1980	28.1	16.1	*	*	*	*	28.1	5.7	82.3	57.5	70.0	476.6	98.0	38.2	8	11		5	.860
	mean	22.7	12.8	*	*	*	*	28.3	6.4	82.1	57.2	69.8	483.3	97.0	37.3	8	12		6	.886
Gilgil	1969	*	*	*	*	*	*	*	*	*	*	*	53.3	110.0	*	6	10		*	*
	1970	*	*	*	*	*	*	*	*	*	*	*	957.5	112.0	*	5	8		*	*
	1971	*	*	*	*	*	*	*	*	*	*	*	637.5	93.0	*	7	10		*	*
	1972	*	*	*	*	*	*	*	*	*	*	*	665.1	123.0	*	7	11		*	*
	1973	*	*	*	*	*	*	*	*	*	*	*	619.5	96.0	*	5	10		*	*
	1975	*	*	*	*	*	*	*	*	*	*	*	712.6	86.0	*	5	9	1768	*	*
	1976	*	*	*	*	*	*	*	*	*	*	*	472.3	69.0	*	6	10		*	*
	1977	*	*	*	*	*	*	*	*	*	*	*	853.2	102.0	*	6	10		*	*
	1978	*	*	*	*	*	*	*	*	*	*	*	678.6	70.0	*	6	7		*	*
	1979	*	*	*	*	*	*	*	*	*	*	*	634.4	61.0	*	6	11		*	*
	1980	*	*	*	*	*	*	*	*	*	*	*	478.7	37.0	*	9	11		*	*
	mean	25.5	10.6	17.3	*	*	*	*	*	*	*	*	729.8	87.2	*	4	11		11	.907

Table 3.5 (continued) Year by year climatic data for baboon sites.

		Temperature (°C)								Relative humidity (%)			Rainfall (mm)			Months with rainfall <		Altitude	Seasonality	
		monthly			daily			absolute													
site	year	max	min	mean	max	min	mean	max	min	a.m.	p.m.	mean	total	days	max	50mm	100mm	(m)	p>2t	z
Assirik	1976	35.6	23.9	29.8	*	*	*	*	*	*	*	*	891.0	74.0	*	3	8		6	.839
	1977	36.1	24.5	30.3	*	*	*	*	*	*	*	*	824.0	79.0	*	7	8		4	.781
	1978	35.8	23.9	23.9	*	*	*	*	*	*	*	*	1124.0	102.0	*	7	7	150	5	.792
	1979	36.0	24.4	30.2	*	*	*	*	*	*	*	*	879.0	82.0	*	6	8		6	.809
	mean	35.9	24.2	30.1	*	*	*	*	*	*	*	*	953.9	84.3	*	3	7		5	.817
Budongo	1972	28.3	14.1	22	*	*	*	*	*	*	*	*	1886.0	*	*	10	9	1015	10	.886
Ruaha		*	*	21.7	*	*	*	*	*	*	*	*	304.0	*	*	3	1	1230	3	.718
Chololo		32.3	11.9	22.1	*	*	*	*	*	*	*	*	597.0	*	*	8	9	1661	5	.846

Table 3.6. Time budget data corrected from Dunbar (1992*b*; table 2: 37).

Site	Time budget %				Dry season feed (%)	Group size	Day Journey / km
	Feed	Move	Rest	Social			
Assirik	23.5	36.9	20.7	18.9	33.1	247.0	7.9
Shai	20.3	18.2	61.4	22.7	22.3	23.7	1.3
Bole	20.5	25.4	35.4	15.9	30.5	19.0	1.2
Mulu	40.8	25.0	22.4	14.7	*	22.0	1.1
Awash	30.9	25.0	30.5	12.2	35.3	71.0	5.3
Budongo	59.3	17.6	5.9	16.9	*	37.5	3.8
Chololo**	40.2	35.8	14.7	7.8	39.0	102.0	5.6
Gilgil	50.7	30.4	9.6	9.3	*	57.0	*
Amboseli	48.0	24.1	20.9	6.7	51.0	48.5	6.1
***Alto's	44.8	25.1	20.9	9.2	*	64.9	4.7
***Hook's	48.1	27.0	16.3	8.6	*	53.4	5.4
***Lodge	23.7	19.2	43.8	13.3	*	48.2	*
***Mean	38.9	23.8	27.0	10.4	*	55.5	10.1
Gombe	25.8	19.4	30.2	10.6	28.1	43.0	*
Ruaha	47.4	24.2	16.7	4.5	*	72.0	*
Mikumi	36.5	26.1	25.0	5.9	38.6	120.0	3.4
Giants Castle	56.6	17.7	16.8	7.7	57.6	11.8	*
Cape	33.5	29.0	2.3	11.3	31.5	85.0	8.2

* no available data

** data corrected from Dunbar 1992, moving and resting time values interchanged.

*** new data from Bronikowski & Altmann (1996).

Table 3.7. Climate data are from a variety of sources, emphasising accuracy of site reference, therefore short-term and long-term data are combined. Data rows in bold type contain long-term data, the remaining rows are study year data.

Site	Temperature / °C			Rainfall	Number of months rainfall with		Seasonality				
	max	min	mean	total	<50mm	<100mm	P>2t	Z	DIV	Alti-tude /m	Latit-ude
Assirik	**35.9**	**24.2**	**30.1**	**963.9**	**3**	**7**	**5**	**.817**	**1.286**	**150**	**9.20**
Bole	22.0	10.1	15.8	1043.3	6	5	7	.828	1.222	2354	9.25
Mulu	22.0	10.1	15.8	1043.3	6	5	7	.828	1.222	2354	9.25
Awash	33.0	18.0	25.0	517.0	9	10	4	.860	1.061	400	8.53
Budongo	28.3	14.1	22.0	1886.0	2	9	10	.894	0.814	1015	1.45
Chololo	32.3	11.9	22.1	531.9	8	9	5	.846	1.107	1661	0.16
Gilgil	**25.5**	10.6	**17.3**	**731.0**	**3**	**11**	**11**	**.916**	**0.513**	**1768**	**0.30**
Amboseli	**31.9**	**14.2**	**23.1**	**225.0**	**11**	*	*	**.820**	*	**1127**	**2.40**
Gombe	**28.0**	**19.0**	**23.5**	**1417.0**	**4**	**6**	**8**	**.884**	**0.951**	**680**	**4.40**
Ruaha	*	*	21.7	298.2	3	1	3	.718	1.550	1230	7.23
Mikumi	**30.1**	**18.6**	**24.3**	**892.0**	**5**	**9**	**6**	**.865**	**1.010**	**579**	**7.15**
Giants Castle	22.7	12.8	16.5	483.17	4	0	6	.890	0.812	12	29.2
Cape	22.7	12.8	16.5	483.17	4	0	6	.890	0.812	12	34.15

* Missing data Sources of climate data. **Assirik**: McGrew *et al.*(1988); **Bole, Mulu & Awash**: nearest weather station for study period (see table 3.3); **Budongo**: Aldridge-Blake (1972); **Chololo**: Barton (1989); **Gilgil**: Kekopey weather station records Dunbar (*pers comm.*); **Amboseli** : Bronikowski & Altmann (1996); **Gombe**: McGrew *et al.* (1988); **Ruaha** (J. Oliver & A. Collins *pers comm.* cited in Dunbar 1992*b*); **Mikumi**: Anon (1984) 30 year average; **Giants Castled & Cape**: nearest weather station for study period (see table 3.3).

Table 3.8. Corrected climate data from subsidiary samples (B & C) table 2 (Dunbar 1992*b*); corrected from original check-sheets (climate data adjusted). Figures in bold are corrected values, values in brackets are the original values.

Population	Mean Annual rainfall/mm	Months with <50mm rainfall /mm	Rainfall diversity (Z)	Mean annual temperature/°C
B. Subsidiary sample				
Badi	941	7	0.803	29.4
Metahara	**663** (639)	6	0.856	24.5
Awash Station	**575** (666)	8	0.841	24.8
Gilgil (1973)	595	**8** (5)	**0.842** (0.908)	18.1
C. Day Journey Sample				
Erer-Gota	**667** (665)	7	0.858	24.2
Ishasha	1292	2	0.906	22.0
Amboseli (1969)	**712** (380)	5	**0.860** (0.861)	20.0
Honnet	**340** (307)	9	**0.846** (0.843)	24.1
Suikersbosrand	700	*	*	16.0

* missing data

N.B. the mean annual temperature for all values listed in table 2 (Dunbar 1992*b*: 37) is 21.93°C. This is relevent to the calculation of P>2t (2×mean annual temperature = 43.86). Therefore the number of months where rainfall (P) is less than 50mm is a good approximation of a dry month for this sample of data.

3.5.2. Correlations between behavioural and environmental variables.

The first step in developing step-wise regression models is to examine carefully correlation matrices. The relationship between behavioural variables (see table 3.6) and environmental variables from a variety of climatic sources, was investigated. The first aim of the reanalyses of Dunbar's (1992*b*) model, was to investigate the effect of the proximity of climate data to the baboon field site, and the period over which the climatic data were collected (long-term versus short-term climate data). Four sources of climate data were evaluated: (1) Study year data from Dunbar 1992*b* (table 3.1); (2) Long term data (Anon 1984; table 3.3); (3) Study year data only, from Anon (1984) (table 3.4); (4) Mixture of long- and short-term climate data, emphasising proximity of the weather station to the baboon field site (table 3.7). Table 3.10. tabulates the significant Spearman rank correlations (two tailed, $p<0.10$) for these four climate sources.

It was established in chapter 2 (fig. 2.12, table 2.12) that there were three key dimensions that characterise a in terms of climatic variables: some measure of rainfall, rainfall variability and temperature were required. In the initial correlation matrix, all

environmental variables were included; however restrictions were placed on the number of independent variables when calculating stepwise regression equations (see section 3.4.3.i.). Environmental variables were available for the baboon field sites, that were not assessed in the larger databases examined in chapter 2. These additional variables were; relative humidity, rainy days, and daily and monthly (minimum and maximum) temperatures. Principal components analyses of the climatic data for the 14 core baboon sites were computed (see table 3.9). The small sample sizes for the principal components analysis warrant caution. However the results assist the comparison of the Spearman rank correlations in table 3.10. where different climate databases had different climatic variables.

The climate data from Dunbar (1992*b*) only had two dimensions, rainfall and dry months, against temperature and rainfall diversity. The long-term climate data had four dimensions, although the fourth (rainy days) was not a robust principal component (% Variance = 6.7%). The remaining three dimensions matched those in chapter 2 (table 2.12); temperature (including altitude), rainfall diversity (including relative humidity), and rainfall. The study-year climate similarly revealed three dimensions; rainfall diversity and temperature. Although the third dimension was Mo100 (number of months with <100mm rain), not rainfall. The mixture of long- and short-term climate again had the same three dimensions as table 2.12; temperature (including altitude), rainfall diversity and rainfall. Therefore, despite the increased number of variables available from the weather station literature compared to the study site data, the habitat can economically be described by three variables. This is relevant to the selection of independent variables for multiple regression models.

The correlation matrices between behavioural and environmental variables were examined first before constructing multiple regression equations (see appendix II; part 1). The sample size for climate sources 1-3 (table 3.9 & 3.10) was 13. This was because there were no weather stations near to field site, Shai Hills. The Shai Hills site was studied over a short period and environmental data cited in Dunbar (1992*b*) are from Depew (1983).

In the following section I shall discuss the initial correlations between environmental and behavioural equations, and will discuss these relationships further in relation to the multiple regression equations. Where there was a significant correlation, feeding time was significantly correlated with Simpson's index of rainfall diversity (*Z*) and temperature (*T*). For the Dunbar (1992*b*) correlations, T and Z were both in the same principal component, and were themselves highly correlated, and therefore would both be expected to appear together. The relationship between feeding time and temperature is negative, reflecting the costs of thermoregulation which rise linearly with declining temperatures (Kleiber 1960; Tokura *et al.* 1975; Mount 1979). Moving time is correlated with Mo50 (number of months with <50mm rainfall) (Dunbar 1992*b*) and relative humidity (long-term climate). Relative humidity falls into the same principal component as Mo50 for the long-term climate data. The number of dry months is highly correlated with productivity (see section 2.4.3): the more productive the habitat, the higher percentage of the day can be spent moving. Resting time is related to a different variable in each of the four climate data bases, although all relate, indirectly, to the amount of cover in the habitat. High heat loads would force the animals to rest in preference to foraging. The relationship between social time and rainfall, for all four of the climate databases, suggests that animals can afford to spend more time resting in richer habitats. The amount of time spent feeding in the dry season is distinguished from overall feeding time, by being related to the number of dry months as opposed to temperature. Day journey length is negatively correlated with rainfall. In richer habitats, animals do not have to move so far in a day to meet their energetic and nutritional requirements.

Table 3.9. Principal components analysis of environmental variables from the four sources of climate data

	Principal components analysis			
Climate data	Factor 1	Factor 2	Factor 3	Factor 4
(1) Dunbar (1992*b*) climate	P, MO50	T, Z	*	*
Eigenvalue	1.84	1.49		
% Variance	46.1	37.2		
Cumulative % variance	46.1	83.2		
(2) Long term climate	TABMAX, TABMIN, TDAMAX, TDAMIN, TDAX, TMOMAX, TMOMIN, TMOX, Z, ALT, P2T	RHUM, RHUMPM, RHUMAM, DIV, MO100, MO50	P	PDAYS
Eigenvalue	8.83	4.79	2.93	1.27
% Variance	46.5	25.2	15.4	6.7
Cumulative % variance	46.5	71.7	87.1	93.8
(3) Study year climate	MO50, P2T, P, Z	ALT, RHUMX, TMOMAX, TMOMIN, TMOX	MO100	*
Eigenvalue	5.69	3.14	1.17	
% Variance	57.0	31.4	11.7	
Cumulative % variance	57.0	88.3	100.0	
(4) Short-and long- term climate	ALT, P2T, TMAX, TMIN, TX	DIV, MO100, MO50, Z	P	*
Eigenvalue	4.41	3.12	1.94	
% Variance	44.1	31.2	19.4	
Cumulative % variance	44.1	75.3	94.7	

* Factor not applicable.

Environmental variables:

Mo50 = number of months with <50mm rainfall; ***Mo100*** = number of months with <100m rainfall; ***P2T*** = number of months where rainfall (mm) is greater than twice the mean annual termperature (°C); ***P*** = rainfall (mm); ***PDAYS*** = number of rainly days; ***Z*** = Simpson's index of rainfall diversity; ***ALT*** = altitude (m); ***RHUMX*** = mean daily relative humidity (%); ***RHUMPM*** = mean relative humidity, p.m. (%); ***RHUMAM*** = mean relative humidity, a.m. (%); ***DIV*** = rainfall diversity index; ***TABMAX*** = mean absolute maximum temperature (°C); ***TABMIN*** = mean absolute minimum temperature (°C); ***TDAMAX*** = mean daily maximum temperature (°C); ***TDAMIN*** = mean daily minimum temperature (°C); ***TDAX*** = mean daily temperature (°C); ***TMOMAX*** = mean maximum monthly temperature (°C); ***TMOMIN*** = mean minimum monthly temperature (°C); ***TMOX*** = mean monthly temperature (°C); ***TMAX*** = mean maximum annual temperature (°C); ***TMIN*** = mean minimum annual temperature (°C); ***TX*** = mean annual temperature (°C).

Table 3.10. Spearman rank correlations (r_s) between behavioural and environmental variables.

Behavioural variable	Environmental variable	r_s	N	p
(1) Dunbar 1992b climate data				
Feed	T	-0.555	14	0.061
	Z	0.502	14	0.067
Move	MO50	0.512	14	0.061
Rest	T	0.466	14	0.093
	Z	-0.576	14	0.031
Social	P	0.515	14	0.060
	MO50	-0.556	14	0.039
Dry Feed	MO50	0.595	10	0.070
N	P	-0.599	14	0.024
	T	0.484	14	0.079
	MO50	0.636	14	0.014
DJL	P	-0.722	14	0.004
	MO50	0.717	14	0.004
(2) Long term climate				
Feed	Z	0.487	13	0.091
Move	RHUM	-0.559	13	0.047
Rest	Z	-0.546	13	0.054
Social	P	0.497	13	0.084
Dry Feed	MO100	0.737	8	0.037
N	RHUMAM	0.072	13	0.072
DJL	P	0.542	9	0.056
(3) Study year climate				
Feed	*	*	*	*
Move	*	*	*	*
Rest	RHUMX	-0.795	6	0.059
Social	RHUMAM	-0.795	6	0.059
	P	0.589	13	0.034
Dry Feed	P	-0.635	8	0.091
N	TMOMAX	0.719	12	0.008
	TMOMIN	0.086	12	0.086
	TMOX	0.020	13	0.020
	P2T	-0.520	12	0.083
DJL	*	*	*	*
(4) Short- and long-term climate				
Feed	*	*	*	*
Move	*	*	*	*
Rest	MO50	0.591	13	0.031
Social	P	0.589	13	0.034
Dry Feed	MO100	0.754	6	0.084
	P	-0.645	8	0.091
N	P2T	-0.519	12	0.083
	TMAX	0.719	12	0.008
	TX	0.634	12	0.020
DJL	P	-0.762	9	0.017

* No significant Spearman rank correlation.

Behavioural variables: ***Feed*** = % feeding time; ***Move*** = % moving time; ***Rest***: % resting time; ***Social*** = % social time; ***DryFeed*** = dry season feeding time %; ***N*** = group size; ***DJL*** = day journey length (km).

Environmental variables: ***RHUMX*** = mean relative humidity (%); ***RHUMAM*** = relative humidity, a.m. (%); ***P*** = mean annual rainfall (mm); ***TMOMAX*** = mean monthly maximum temperature (°C); ***TMOMIN*** = mean monthly minimum temperature (°C); ***TMOX*** = mean monthly temperature (°C); ***P2T*** = number of months where rainfall (mm) is greater than twice the mean annual temperature (°C); ***TMAX*** = mean maximum annual temperature (°C); ***TX*** = mean annual temperature (°C); ***Z*** = Simpson's index of rainfall diversity; ***MO50*** = number of months with <50mm rainfall; ***MO100*** = number of months with <100mm rainfall.

3.5.3. Determinants of the time budget

i. Comparison of equations from Dunbar (1992b; 1996), Bronikowski & Altmann (1996), and corrections to Dunbar (1992b).

Multiple regression equations presented in Bronikowski & Altmann (1996), Dunbar (1992*b*, 1996) and this thesis, of behavioural on meteorological variables are presented in table 3.11. Regression equations are shown that account for a significant proportion of the variance in the four time budget variables and day journey length. The same behavioural data are used in each analysis, except for this thesis, where the data corrections are taken account of (see tables 3.6 and 3.8) and where Altmann & Bronikowski have corrected the Amboseli data. The differences between Bronikowski & Altmann equations and Dunbar's equations may therefore be partly accounted for by statistical technique, since the data are identical. All data are log transformed to fulfil the assumption of normal distribution of data in multivariate analyses. The arc sine transformation suggestion for proportional data was not used so that equations were comparable.

Discussion

Table 3.11. compares the equations from Bronikowski & Altmann (1996), Dunbar (1992*b*; 1996) and those generated in this thesis from the corrected data. Day journey length is a positive function of group size in all four equations, and a negative function of rainfall. The relationship between day journey length and group size may be explained, if it is assumed that each individual group member forages in a constant area per day. If rainfall indexes resource density, or patchiness, this would influence day journey length. A further suggestion is that rainfall indexes the amount of available surface ground water. Water is a significant factor influencing baboon ranging patterns (Altmann & Altmann 1970; Sigg & Stolba 1981; Barton 1989). The equation derived from the corrected data, differs only that *V* (number of months with less than 50mm rainfall) is included in the equation. *V* indexes plant productivity, therefore habitat patchiness, which would determine day journey length.

Table 3.11. Comparison of time budget equations from the same behavioural data, comparing equations presented in Dunbar (1992*b*, 1996); Bronikowski & Altmann (1996) and this study.

Analysis	Multiple regression equation*	*R2*	*F(df)*	*P*
Day journey length /km2 (D)				
Bronikowski & Altmann	$\ln(D)=2.68+0.68(N)-0.61\ln(P)$	0.72	21.59(2,14)	<0.001
Dunbar (1992)	$\ln(D)=1.34+0.78\ln(N)-0.47\ln(P)$	0.69	18.87(2,18)	<0.001
Dunbar (1996)	As 1992			
This thesis	$\ln(D)=-2.183 + 0.401\ln(V) + 0.691\ln(N)$	0.81	6.56(2,7)	0.025
Feeding time (%) (F)				
Bronikowski & Altmann	$\ln(F)=6.39+5.12\ln(Z)-0.68\ln(T)$	0.37	4.82(2,11)	<0.05
Dunbar (1992)	$\ln(F)=7.41+4.44\ln(Z)-0.88\ln(T)-0.45\ln(V)+0.16\ln(D)$	0.58	3.15(4,9)	<0.06
Dunbar (1996)	a) $\ln(F)=6.87+4.08\ln(Z)-0.75\ln(T)-0.39\ln(V)+0.16\ln(D)$ (for T<30°C) b) $\ln(F)=1.77+4.08\ln(Z)+0.75\ln(T)-0.39\ln(V)+0.16\ln(D)$ (for T>30°C)			
This thesis	$\ln(F)=6.187 + 3.886\ln(Z) - 0.667\ln(T)$	0.63	3.67 (2,11)	0.06
Moving time (%) (M)				
Bronikowski & Altmann	$\ln(M)=2.15+0.15\ln(N)+0.28\ln(V)$	0.64	12.34(2,11)	<0.005
Dunbar (1992)	$\ln(M)=2.21+0.16\ln(N)+0.22\ln(V)$	0.66	10.68(2,11)	<0.01
Dunbar (1996)	As 1992			
This thesis	$\ln(M)=2.195 + 0.195\ln(V) + 0.172\ln(N)$	0.79	9.16(2,11)	0.0045
Resting time (%) (R)				
Bronikowski & Altmann	$\ln(R)=7.57-1.26\ln(F)$	0.63	23.48(1,12)	<0.001
Dunbar (1992)	$\ln(R)=10.55-1.33\ln(F)-0.32\ln(N)-0.28\ln(P)$	0.78	11.98(3,10)	<0.01
Dunbar (1996)	$\ln(R)=0.97-7.92\ln(Z)+0.60\ln(V)$			
This thesis	$\ln(R)=8.609 - 1.415\ln(F) - 0.859\ln(T)+1.718\ln(Z)+ 0.362\ln(P)$	0.86	5.18(4,7)	0.029
Social time (%) (S)				
Bronikowski & Altmann	$\ln(S)=1.15+0.47\ln(P)-0.54\ln(F)$	0.50	5.50(2,11)	<0.01
Dunbar (1992)	$\ln(S)= -1.60+0.49\ln(P)-4.96\ln(Z)$	0.53	6.31(2,11)	<0.02
Dunbar (1996)	$\ln(S)= -2.28+1.32\ln(Z)-0.04(\ln(N))2$			
This thesis	$\ln(S)= 4.837 - 0.684\ln(F)$	0.53	4.77(1,12)	0.049

* D = day journey length (km); N = group size; P = mean annual rainfall (mm); V = number of months with <50mm rainfall (or Mo50); Z = Simpson's index of rainfall diversity; T = mean annual temperature (°C).

The feeding time equations in Dunbar (1992*b*) and Bronikowski & Altmann (1996) are determined primarily by temperature and rainfall diversity (*Z*). The exclusion of dry months (*V*) and day journey length (*D*) from Bronikowski & Altmann's equations might be due to different inclusion criteria. However, lenient criteria were used by Bronikowski & Altmann (FIN = 2.0, FOUT = 1.996), therefore at least as many predictors would be expected, not fewer. Dunbar (1992*b*) used even more lenient criteria, including any variables that added at least $r^2 = 0.05$ extra, providing the overall F value was still significant. Dunbar (1996) adjusted the feeding time equation to take into account increasing thermoregulatory costs above 30°C. The model was then refined, such that maximum ecologically tolerable group sizes were not possible above 40°C, because fossorial mammals cannot survive in habitats where mean ambient temperatures exceed 35°C (P.Wheeler *pers comm.* cited in Dunbar 1996). In addition, the feeding time equation was adjusted to take into account increasing thermoregulatory costs at very high temperatures. Energy consumption decreases with increasing temperature, however at ambient temperatures greater 35°C energy consumption rises again (Mount 1979).

There is no significant correlation between temperature and feeding time when the data are corrected from Dunbar (1992*b*) (two-tailed $r_s = -0.328$, n=13, $p=0.27$). When the baboon field sites are divided into low- and high-temperature sites, a significant least squares regression equation could be drawn through the high temperature sites (figure 3.3.a. and table 3.12). Linear, quadratic and cubic regressions were set through the data, none of which yielded significant regression equations (see table 3.12, figure 3.3.b). It is the lack of a significant correlation between feeding and temperature that explains the absence of a significant multiple regression equation in the reanalysis of the baboon socioecology data (see table 3.13.b).

Figure 3.3.a. Graph to show the relationship between feeding time and temperature in 15 baboon field sites. Regression line is shown for a sub-group of higher-temperature sites.

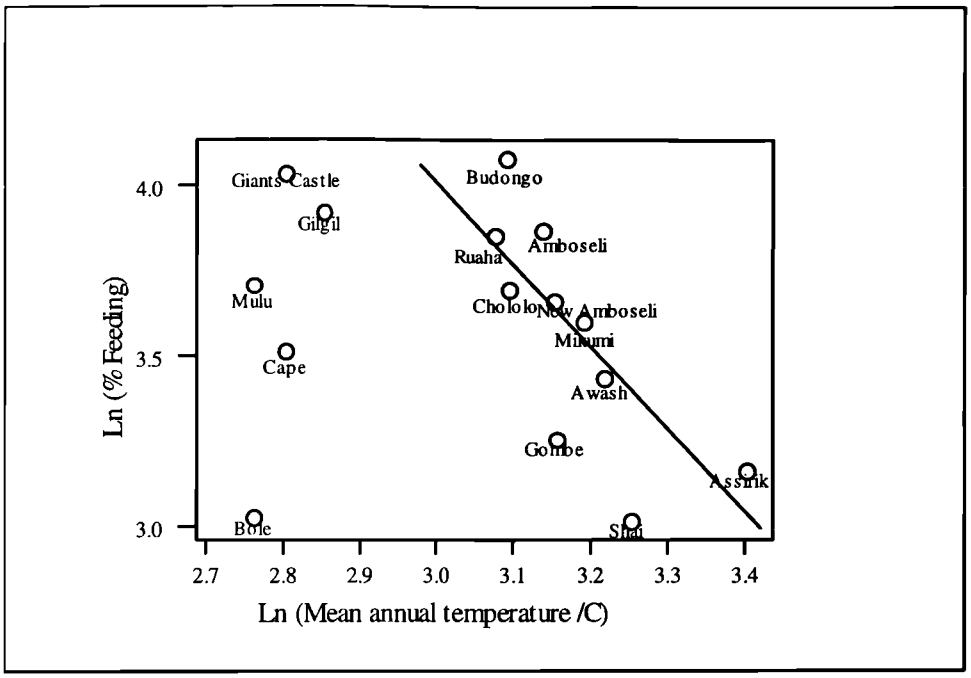
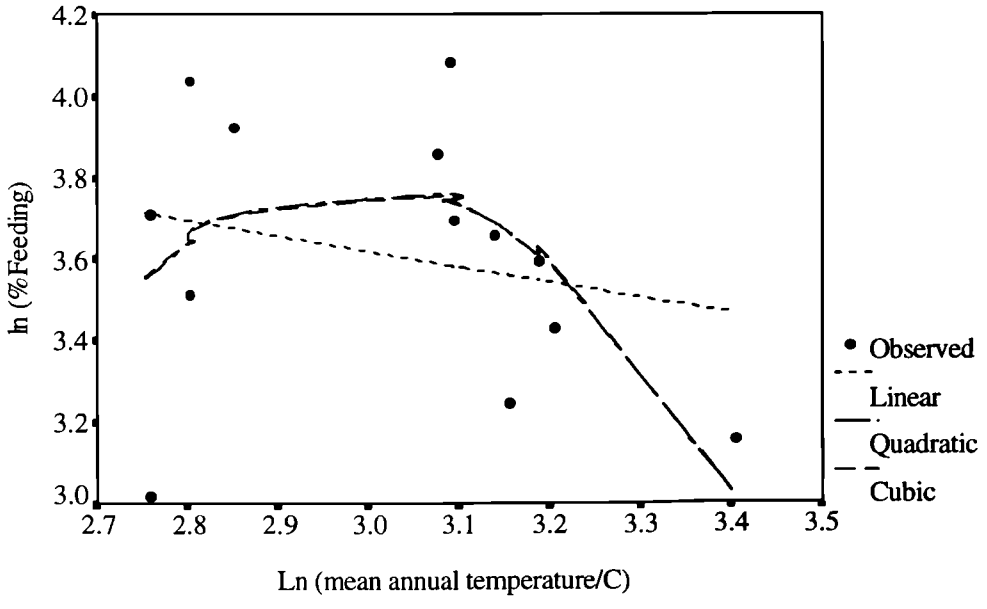


Table 3.12. Multiple regression equations for high and low -temperature sub-groups, and linear, quadratic and cubic equations for all data-points.

	Equation	r^2	*F(df)*	*p*
High temperature*	$\ln(F)=12.2-2.7\ln(T)$	0.59	11.49(1,8)	0.009
Low temperature**	$\ln(F)= -14.8+6.58\ln(T)$	0.38	1.86(1,3)	0.266
Linear	$\ln(F)=3.56-0.15\ln(T)$	0.06	0.66(1,11)	0.434
Quadratic	$\ln(F)= -1.52+2.73\ln(T)-0.40(\ln(T))^2$	0.10	0.55(2,10)	0.593
Cubic	$\ln(F)=0.35+1.22\ln(T) -0.40(\ln(T))^2-0.04(\ln(T))^3$	0.10	0.55(2,10)	0.609

***High temperature sites:** Budongo, Ruaha, Amboseli, Cholollo, Mikumi, Awash, Gombe, Assirik, Shai.
****Low temperature sites:** Giants Castle, Gilgil, Mulu, Cape, Bole.

Figure 3.3.b. Linear, quadratic and cubic regressions set through feeding time against mean annual temperature.



The moving time equation was found to be very similar in the re-analysis to the equations presented in Bronikowski & Altmann (1996). The equation generated in this thesis did not include group size as a predictor variable. Two hypotheses were put forward by Dunbar (1992*b*) to explain the relationship between moving time and group size. Firstly, that larger groups have longer day journeys (see day journey length equations) and secondly that larger groups experience more interruptions in feeding bouts, and therefore have to move more frequently to find new feeding patches. The inclusion of rainfall diversity in the moving time equation suggests that it is resource patchiness (as indexed by rainfall diversity) that influences moving time, by short changes in feeding site, as opposed to major episodes of travel (Dunbar 1992*b*).

The resting time equation, originally presented in Dunbar (1992*b*), was logarithmic reaching an asymptotic value. The asymptotic value was 5-10% resting time, which was interpreted as the minimum permissible resting time. The relationship between resting time and rainfall diversity (which indexes the degree of habitat cover), may be interpreted in terms of heat load. In the equation generated in this thesis, temperature is included in the equation. High radiation loads, particularly at midday, are documented to force animals to spend time resting, rather than foraging, and to actively seek shade during resting periods (e.g. Altmann & Altmann 1970; Stoltz & Saayman 1970; Stelzner 1988).

The only significantly different time budget equation in Bronikowski & Altmann's reanalysis was for social time. In their equation, feeding time entered the equation, but did not in either of Dunbar's equations. However, Dunbar (1992*b*) asserts that the available time for socialising and resting was limited by the amount of time that had to be spent feeding in order to survive. Since social time is related to rainfall and rainfall diversity, social time increases in richer habitats, where less time may be spent devoted to feeding.

To summarise, given the correction of data, inclusion of new data, and slightly different statistical inclusion criteria for stepwise regression, there are very few

significantly different functional equations. Particularly, given the relatively small sample size, the functional relationship derived from multiple regression seem to be relatively robust, and fulfil the criteria for a successful equation; biological plausibility.

ii. Comparing equations from different statistical inclusion criteria for multiple regression.

Table 3.13.a. compares the time budget equations using the corrected data from Dunbar (1992*b*) but for different statistical inclusion criteria for the stepwise multiple regression model. Again, qualitatively, regardless of the inclusion criteria, the equations are functionally the same as those generated in Dunbar (1992*b*).

This finding highlights the robusticity of the equations; biologically, similar functional equations are derived from different statistical criteria for stepwise multiple regression.

iii. Comparison of long-term, short-term climate data and mixed climate data

Table 3.13.b. lists four equations for each of the five behavioural categories; moving time, resting time, social time, feeding time and day journey length. The first two equations were computed from the corrected Dunbar (1992*b*) data, but using different FIN and FOUT values for the step-wise regression equations in SPSS 6.0 for Windows. Again, qualitatively, the equations are very similar to one another, and to the equations in table 3.10.

Table 3.13.a. Table to compare equations derived from re-analysis of Dunbar (1992*b*).

Database	Multple regression equation*	R2	F(*df*)	*P*
Day Journey Length / km2 (D)				
Dunbar (1992) corrected FIN(2.0) FOUT (1.996)	$\ln(D) = -0.602 - 0.301\ln(R) + 0.674\ln(N)$	0.89	13.41(2,7)	0.004
Dunbar (1992) corrected FIN(4.0) FOUT (4.0)	As above	As above	As above	As above
Feeding Time (%) (F)				
Dunbar (1992) corrected FIN(2.0) FOUT (1.996)	$\ln(F)=9.366+7.611\ln(Z)-0.193\ln(P)-1.454\ln(T)-0.346\ln(V)+0.428\ln(N)$	0.98	11.85(5,3)	0.034
Dunbar (1992) corrected FIN(4.0) FOUT (4.0)	$\ln(F)=6.39 - 0.434\ln(P)$	0.65	5.14(1,7)	0.056
Moving Time (%) (M)				
Dunbar (1992) corrected FIN(2.0) FOUT (1.996)	$\ln(M)=3.943 - 0.245\ln(F)+0.65\ln(V)-0.287\ln(R)$	0.98	50.96(3,5)	0.0004
Dunbar (1992) corrected FIN(4.0) FOUT (4.0)	As above	As above	As above	As above
Resting Time (%) (R)				
Dunbar (1992) corrected FIN(2.0) FOUT (1.996)	$\ln(R)=7.89-1.36\ln(F)$	0.81	13.18(1,7)	0.092
Dunbar (1992) corrected FIN(4.0) FOUT (4.0)	As above	As above	As above	As above
Social Time (%) (S)				
Dunbar (1992) corrected FIN(2.0) FOUT (1.996)	$\ln(S)=4.69-0.618\ln(F)-1.70\ln(V)-10.584\ln(Z)$	0.83	3.81(3,5)	0.092
Dunbar (1992) corrected FIN(4.0) FOUT (4.0)	$\ln(S)=4.99-0.733\ln(F)$	0.56	5.54(1,12)	0.037

Table 3.13.b. Table to compare equations from short-term climate data (see tables 3.4 & 3.5) and long-term climate data (see tables 3.2 & 3.3)

Database	Multple regression equation*	R2	F(*df*)	*P*
Day Journey Length / km2 (D)				
Dunbar (1992) short-term climate data	$\ln(D) = 12.875 + 0.397 \ln(N) - 1.64 \ln(P) - 1.29 \ln(V)$	0.95	15.42 (3,5)	0.006
Dunbar (1992) long-term climate data	$\ln(D) = -1.59 + 0.725 \ln(N)$	0.74	8.67 (1,7)	0.022
Dunbar(1992) mixed climate data	$\ln(D) = -1.590 + 0.724 \ln(N)$	0.74	8.67 (1,7)	0.022
Feeding Time (%) (F)				
Dunbar (1992) short-term climate data	$\ln(F) = 3.565 - 0.149 \ln(T)$	0.06	0.66 (1,11)	0.434
Dunbar (1992) long-term climate data	$\ln(F) = 4.22+4.04 \ln(Z)$	0.50	3.83 (1,11)	0.071
Dunbar(1992) mixed climate data	$\ln(F) = 4.745 - 0.351 \ln(T) + 0.441 \ln(Z)$	0.25	0.34 (2,10)	0.718
Moving Time (%) (M)				
Dunbar (1992) short-term climate data	$\ln(M) = 2.433 + 0.199 \ln(N)$	0.70	10.72 (1,11)	0.0074
Dunbar (1992) long-term climate data	$\ln(M) = 2.433 + 0.199 \ln(N)$	0.70	10.72 (1,11)	0.0074
Dunbar(1992) mixed climate data	$\ln(M) = 4.717 + 0.139 \ln(R) + 0.44 \ln(N)$	0.91	15.358 (3,9)	0.0007
Resting Time (%) (R)				
Dunbar (1992) short-term climate data	$\ln(R) = -6.683 - 13.52 \ln(Z) - 0.514 \ln(D) + 2.56 \ln(T)$	0.87	5.13 (3,5)	0.055
Dunbar (1992) long-term climate data	$\ln(R) = 6.35 - 0.98 \ln(F)$	0.64	3.42 (2,1)	0.070
Dunbar(1992) mixed climate data	$\ln(R) = 4.355 - 0.700 \ln(F) + 0.626 \ln(V)$	0.57	2.42 (2,10)	0.138
Social Time (%) (S)				
Dunbar (1992) short-term climate data	$\ln(S) = 1.59 + 0.339 \ln(P) - 0.408 \ln(F)$	0.63	3.25 (2,10)	0.082
Dnbar (1992) long-term climate data	$\ln(S) = -1.23 + 0.804 \ln(P) - 0.514 \ln(F)$	0.64	3.42 (2,10)	0.074
Dunbar(1992) mixed climate data	$\ln(S) = -0.139 + 0.380 \ln(P)$	0.55	4.68 (1,11)	0.053

*see legend in table 3.10.

The long-term climate data enables a feeding time equation to be generated, the independent climatic variables are more normally distributed in the long- versus the short-term climate data.

Table 3.14. lists the functional equations generated from the long-term climate data available in the H.M.S.O. compilation (Anon 1984) (see tables 3.2 & 3.3). Additional climatic variables were available in this data base (relative humidity, maximum and minimum temperature). However, as shown in chapter 2 (see section 2.4.5.), only three key environmental variables (temperature, rainfall, temporal distribution of rainfall), economically distinguished habitats. Therefore the additional climatic variables available in this database were not utilised in the final model of maximum ecologically tolerable group size.

Table 3.14. Stepwise regression equations for baboon time budgets, using climate data from H.M.S.O. compilation (Anon 1984; see tables 3.2 & 3.3).

Dependent variable	Multiple regression equation*	R^2
Day Journey Length / km² ***(D)***	ln(***D***)=3.04-0.62ln(***F***)	0.31
Feeding Time (%) (F)	ln(***F***)=2.57-0.38ln(***N***)-0.41ln(***P***)	0.87
Moving Time (%) (M)	ln(***M***)=2.24-3.22ln(***Z***)+0.24ln(***TMIN***)	0.95
Resting Time (%) (R)	ln(***R***)=19.84-2.25ln(***M***)-1.83ln(***S***)-4.81ln(***RH***)	0.95
Social Time (%) (S)	ln(***S***)= -4.29+1.87ln(***MAXT***)	0.43

* Dependent variables used in the equations: Monthly mean temperature (°C) ***T***; maximum temperature ***TMAX***; minimum temperature ***TMIN***; mean relative humidity (%) ***RH***; mean annual rainfall (mm) ***P***; number of months with less than 50mm rainfall ***V***; Simpson's index of rainfall diversity ***Z***.

The moving time equation includes minimum temperature as a predictor variable, reflecting the thermoregulatory costs of moving. The resting time equation does not contain temperature, but relative humidity. Social time is positively related to maximum temperature.

The independent variables used to generate the equations in table 3.14 are not comparable to those in the previous analyses. Nevertheless similarities can be seen in terms of the biological function of the explanatory variables in the equations. This supports the decision, based on the ecological correlations in chapter two; that relatively

few ecological variables are sufficient to explain a large proportion of the variance in time budgets.

3.5.4. Summary of results

Climatic data for the baboon field sites was collected from four different sources. The four climate sources were as follows: (1) Long-term records from nearby weather stations; (2) study-year data from nearby weather stations; (3) field site climate for study years, and; (4) a mixture of long- and short-term climate data emphasising the accuracy of proximity of the climate data source and the baboon field site. Principal components analyses on the climate data listed for the baboon field sites revealed a similar number of dimensions to the analysis on a larger database in chapter 2 (fig. & table 2.12). Therefore, despite the different climatic variables available in each site, the resulting functional equations with time budget variables could be compared.

Functionally, the step-wise multiple regression equations generated from the same time budget data, for each of the four climate data sources were very similar. Therefore the relationships between climatic and behavioural variables are relatively robust in relation to the accuracy of the proximity of the climate data to the behavioural data source, and the duration of the climate data.

In the following section I shall assess how well the functional equations generated from the different climate sources, and from different statistical inclusion criteria for step-wise regression, predict the time budgets in the subsidiary sample.

3.6. TESTING THE EQUATIONS

3.6.1. Predicting time budgets

A series of functional equations have been presented in tables 3.11, 3.12a & b. and 3.14. Following Dunbar (1992*b*) these equations were derived from a core sample of 14 baboon populations. An independent, subsidiary sample (see table 3.8) of four populations was used to test the equations. Fisher's procedure for combining probabilities from independent tests of significance was used test whether there was a

significant difference between the observed time budgets from the subsidiary sample (n = 4), and the time budgets that would be predicted from the functional equations derived from the core sample (n = 14). Fisher's test allows us to determine whether the predicted time budgets are more similar to the observed time budgets than would be expected by chance. The formula for Fisher's test is; $-2\sum \ln P$ (Sokal & Rohlf 1984: 780). In other words, Fisher's test of combined probabilities was used to assess whether the observed distribution of z-scores was larger than would be expected by chance alone if there were no relationship between the observed and predicted time budgets. For example if the χ^2 value is high, then the difference between the observed and expected values is high. A highly significant χ^2 value shows that there is a significant difference between the observed time budget, and the time budget predicted by the functional equations. A non-significant χ^2 value, by default shows that the observed and expected values are not-significantly different (i.e. are similar).

Table 3.15. compares the observed time budgets with the values that would be predicted by the equations in tables 3.11, 3.12a & b. and 3.14. Table 3.15 lists the observed and expected values, with the number of standard deviations separating these two values (see figures 3.3.a. & b.). The difference between z-scores for observed and expected values in table 3.15 were converted to two-tailed probabilities of the deviation of observed from predicted values (table 3.16). These *p*-values were then used in Fisher's procedure for pooling independent tests to determine whether the observed distribution of z-scores was larger than would be expected by chance if there was no relationship between the observed and expected values. Therefore a non-significant *P*-value for Fisher's test indicates that the observed time budgets are not significantly different from the time budgets predicted from the regression equations.

Fisher's test of combined probabilities was calculated for each time budget, and for each equation (a to h). The two-tailed probabilities in table 3.16 were used to compute Fisher's statistic (table 3.17).

I shall first discuss the number z-scores of the difference between observed and expected time budgets (table 3.15; figures 3.4.a. and b). When comparing the magnitude

of z-scores between the time budget categories, it should be noted that the x-axis scale (z-score) in figures 3.4.a. and b. differs between the time budget categories. For feeding time, the equations b and d (Dunbar 1996; and the equation with statistical inclusion criteria of fin 2.0) had standard deviations greater than one for the four subsidiary baboon sites. For moving time, all the equations for Badi predicted time budgets significantly greater than was observed (see table 3.15), with z-scores greater than 3 standard deviations. The resting time budgets were on the whole accurately predicted. As with moving time, the highest z-scores were for Badi, with the exception of equation b (Dunbar 1996). Finally, for social time the z-scores were highest for equations b and d.

Table 3.15. Comparison of observed time budgets with values predicted by the equations in tables 3.11, 3.12a & b. and 3.14.

Time budget		Feed			Move			Rest			Social		
SD of main sample		13.05			5.35			13.22			13.03		
Population	Equation	O	E	Z	O	E	Z	O	E	Z	O	E	Z
Metahara	a		30.61	0.64		26.57	0.05		26.02	0.18		10.55	0.12
	b		26.63	1.26		11.40	0.25		10.51	0.93		32.23	0.12
	c		32.23	0.51		27.44	0.21		15.91	0.59		10.30	0.08
	d	38.9	4.28	2.66	26.3	27.19	0.17	23.7	18.37	0.40	9.9	0.03	1.88
	e		35.53	0.26		27.19	0.17		18.37	0.40		10.04	0.03
	f		21.94	1.30		27.70	0.26		0.22	1.78		9.83	0.01
	g		36.37	0.19		24.95	0.26		15.83	0.60		18.43	0.01
	h		36.37	0.19		24.31	0.26		18.43	0.40		10.11	0.04
Gilgil	a		34.37	0.97		27.63	1.35		27.04	0.48		10.02	0.41
	b		14.48	2.50		26.92	0.22		29.87	0.64		4.22	1.12
	c		36.13	0.84		24.22	0.71		14.69	0.51		9.04	0.20
	d	47.1	3.10	3.38	20.4	23.74	0.62	21.4	14.15	0.55	10.1	0.08	1.91
	e		37.23	0.76		23.74	0.62		14.15	0.55		8.72	0.26
	f		22.95	1.85		24.95	0.85		0.26	1.60		8.88	0.23
	g		33.96	1.01		24.95	0.85		13.13	0.63		14.38	0.23
	h		30.26	1.01		30.26	1.84		14.31	0.53		9.87	0.04
Awash	a		27.68	0.16		27.72	0.43		27.04	0.33		10.02	0.66
	b		19.10	0.810		27.00	0.30		22.27	0.69		5.60	1.50
	c		29.17	.04		26.52	0.21		21.24	0.77		12.4	0.21
	d	29.7	2.76	2.07	25.4	13.42	2.24	31.4	26.53	0.37	13.5	0.10	2.55
	e		37.80	0.62		13.42	2.24		26.53	0.37		12.24	0.24
	f		21.90	0.60		24.95	0.08		0.18	2.36		11.13	0.45
	g		33.82	0.45		24.95	0.08		20.63	0.81		26.63	0.45
	h		33.82	0.32		31.91	1.22		26.63	0.61		10.29	0.61
Badi	a		30.09	0.37		28.73	3.67		31.82	1.12		13.56	0.43
	b		*	2.00		28.36	3.60		48.04	0.11		0.04	3.00
	c		27.78	0.13		28.05	3.54		24.34	1.68		13.54	0.43
	d	26.1	3.39	1.74	9.1	27.28	3.40	46.6	31.62	1.13	15.8	5.39	1.98
	e		30.52	0.34		27.28	3.40		31.62	1.13		13.45	0.45
	f		21.35	0.36		27.45	3.43		*	3.52		13.97	0.35
	g		28.09	0.35		27.45	3.43		23.41	1.75		28.84	0.61
	h		28.09	0.15		29.43	3.80		26.84	0.77		11.74	0.77

* no day-journey length for Badi sample. **Equations:** **a**: Bronikowski & Altmann (1996); **b**: Dunbar (1996); **c**: This thesis; **d**: fin(2.0) fout(1.996); **e**: fin(4.0) fout(4.0); **f**: short-term climate data; **g**: long-term climate data; **h**: mixed climate data.

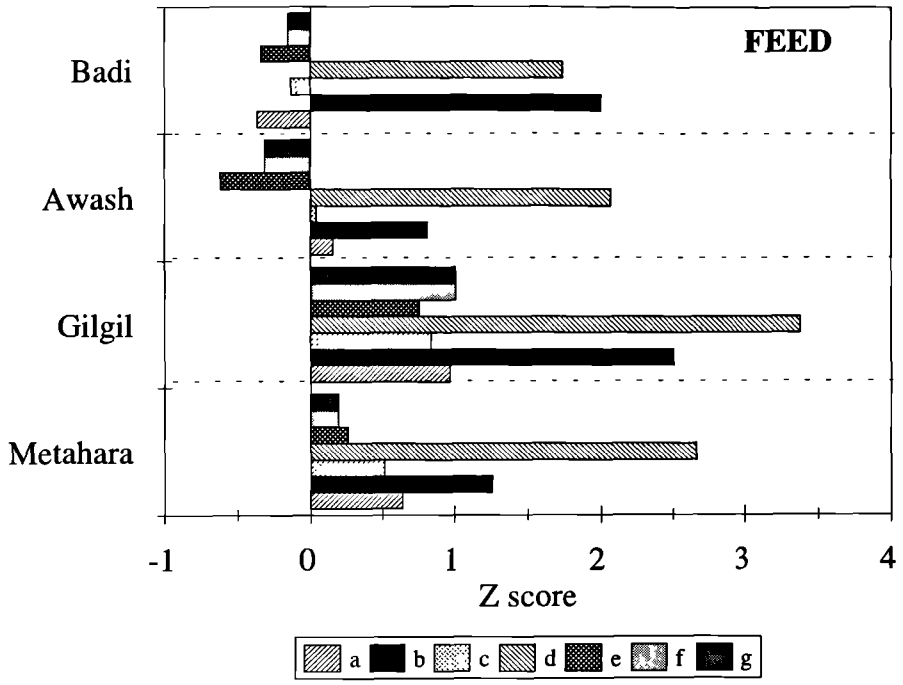
Table 3.16. Two-tailed probabilities of the deviation of observed from expected time budgets computed from equations in tables 3.11, 3.12a & b. and 3.14.

Equation*	Site	Feed	Move	Rest	Social
Equation A	Metahara	0.52	0.96	0.86	0.90
	Gilgil	0.33	0.18	0.63	0.68
	Awash	0.87	0.67	0.74	0.51
	Badi	0.71	0.00	0.26	0.67
Equation B	Metahara	0.21	0.80	0.35	0.90
	Gilgil	0.01	0.22	0.52	0.26
	Awash	0.42	0.38	0.49	0.13
	Badi	*	0.00	0.91	0.00
Equation C	Metahara	0.61	0.42	0.08	0.94
	Gilgil	0.40	0.48	0.61	0.84
	Awash	0.97	0.83	0.44	0.83
	Badi	0.89	0.00	0.09	0.67
Equation D	Metahara	0.01	0.87	0.69	0.06
	Gilgil	0.00	0.54	0.58	0.06
	Awash	0.04	0.03	0.71	0.01
	Badi	0.08	0.00	0.26	0.05
Equation E	Metahara	0.79	0.87	0.69	0.98
	Gilgil	0.45	0.54	0.58	0.80
	Awash	0.54	0.03	0.71	0.81
	Badi	0.73	0.00	0.26	0.65
Equation F	Metahara	0.79	0.87	0.69	0.98
	Gilgil	0.45	0.54	0.58	0.79
	Awash	0.54	0.03	0.71	0.81
	Badi	0.73	0.00	0.26	0.65
Equation G	Metahara	0.85	0.79	0.55	0.99
	Gilgil	0.31	0.40	0.53	0.82
	Awash	0.75	0.94	0.42	0.65
	Badi	0.88	0.00	0.08	0.73
Equation H	Metahara	0.85	0.71	0.69	0.97
	Gilgil	0.31	0.07	0.60	0.97
	Awash	0.75	0.22	0.72	0.54
	Badi	0.88	0.00	0.14	0.44

* no day-journey length for Badi sample.

Equations: **a**: Bronikowski & Altmann (1996); **b**: Dunbar (1996); **c**: This thesis; **d**: fin(2.0) fout(1.996); **e**: fin(4.0) fout(4.0); **f**: short-term climate data; **g**: long-term climate data; **h**: mixture of climate data.

Figure 3.4.a. Graphs to show z-scores for the difference between obseved and predicted time budgets for the 4 test sites (see table 3.13)



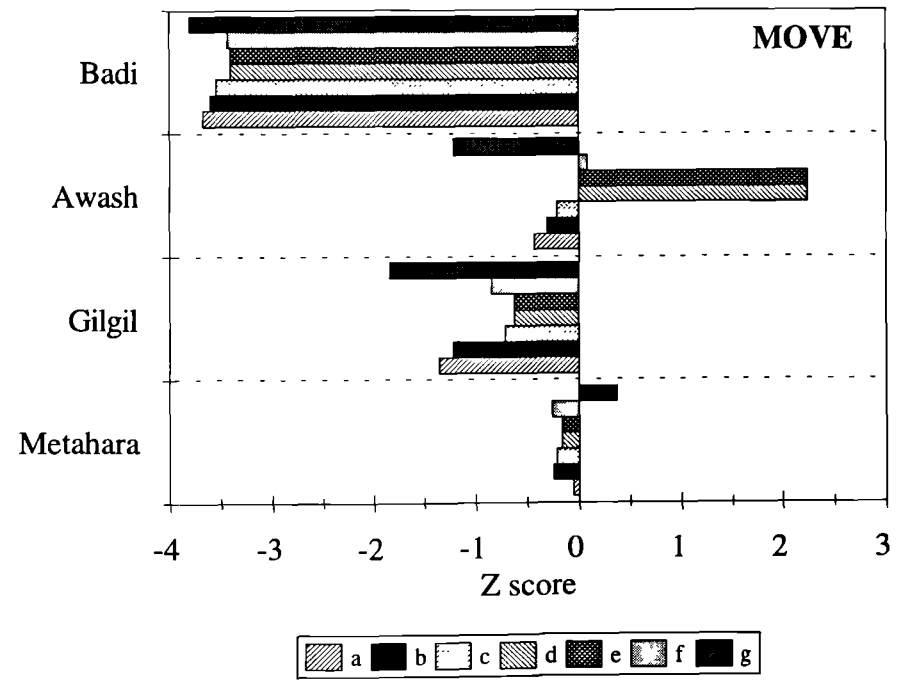
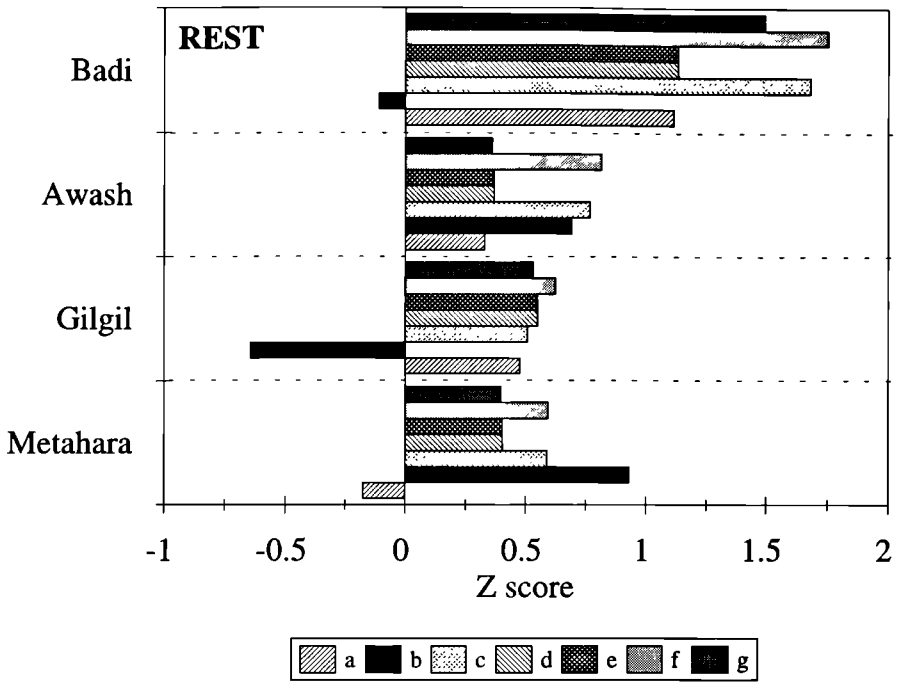


Figure 3.4.b. Graphs to show z-scores for the difference between obseved and predicted time budgets for the 4 test sites (see table 3.13)



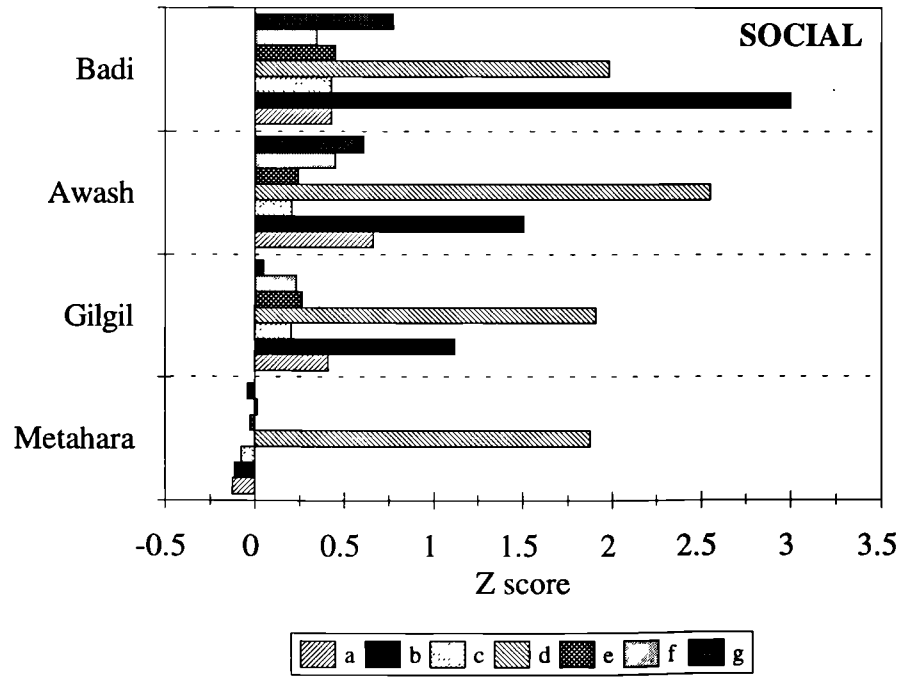


Table 3.17. Fisher's test for combining probabilities from independent tests of significance. Non-significant *P*-values shown in bold type. df = 8 for all tests.

		Time budget			
		Feed	**Move**	**Rest**	**Social**
	sum*	-2.24	-10.16	-2.25	-1.57
A	**x2**	4.48	20.33	4.50	3.14
	p	**>.70**	<.001	**>.80**	**>.95**
	sum	-6.87	-10.73	-2.50	-9.40
B	**x2**	13.73	21.46	4.99	18.80
	p	>.05	<.02	**>.80**	<.05
	sum	-1.56	-9.48	-6.25	-0.83
C	**x2**	3.11	18.95	12.50	1.65
	p	**>.95**	<.02	<.20	**>.99**
	sum	-21.84	-11.88	-2.61	-13.26
D	**x2**	43.68	23.76	5.21	26.52
	p	<.001	<.01	**>.50**	<.001
	sum	-1.97	-11.88	-2.61	-0.89
E	**x2**	3.94	23.76	5.21	1.78
	p	**>.90**	<.01	**>.90**	**>.98**
	sum	-1.97	-11.88	-1.25	-0.89
F	**x2**	3.94	23.76	2.51	1.78
	p	**>.80**	<.01	**>.95**	**>.98**
	sum	-1.97	-8.64	-4.63	-0.96
G	**x2**	3.49	17.28	9.27	1.91
	p	**>.80**	<.02	>.20	**>.98**
	sum	-1.74	-4.57	-3.21	-1.49
H	**x2**	3.49	9.13	6.43	2.99
	p	**>.80**	>.30	**>.70**	**>.90**

*sum = sum of logged P-values for the z-scores of the difference between observed and expected time budgets. **χ^2 = chi-square (Fisher's test: $-2\sum \ln P$).
Equations: **a**: Bronikowski & Altmann (1996); **b**: Dunbar (1996); **c**: This thesis; **d**: fin(2.0) fout(1.996); **e**: fin(4.0) fout(4.0); **f**: short-term climate data; **g**: long-term climate data; **h**: mixture of climate data.

Equations a, b and c (Bronikowski & Altmann 1996; Dunbar 1996; this thesis)

Bronikowski & Altmann's equations predicted feeding and resting and social time accurately ($p>0.70$), whereas predicted moving time was significantly different from the observed value ($p<0.001$). Bronikowski & Altmann's equations differed by their statistical inclusion criteria, and the correction of any errors in Dunbar (1996) and the updating of the Amboseli data. The lack of significance in the moving time equation may be partly explained by the Badi moving time data. None of the equations accurately predicted Badi moving time (see z-scores in figure 3.4.a.). It was noted in Dunbar (1992*b*) that the Badi moving time observed scores may have been lower than expected due to poor field conditions for observing animals on the ground (see Dunbar & Nathan 1972). Table 3.18 shows the results for Fisher's test for moving time only, omitting

Badi moving time. Moving time for equation (a), does become non-significantly different from observed when Badi moving time is removed, similarly for equation (b).

Table 3.18. Fisher's test for combined probabilities. Moving time equations, with Badi moving time omitted (df = 6).

	Moving time Equation							
	A	**B**	**C**	**D**	**E**	**F**	**G**	**H**
sum	-2.18	-2.69	-1.79	-4.46	-4.46	-4.46	-1.22	-4.56
x^2	4.35	5.37	3.59	8.92	8.92	8.92	2.45	9.13
p	>0.50	>0.30	>0.50	>0.10	>0.10	>0.10	>0.80	>0.10

Equations: **a**: Bronikowski & Altmann (1996); **b**: Dunbar (1996); **c**: This thesis; **d**: fin(2.0) fout(1.996); **e**: fin(4.0) fout(4.0); **f**: short-term climate data; **g**: long-term climate data; **h**: mixture of climate data.

Equations (c), are those computed in this thesis, correcting the time budget values for Chololo, adding new data from Amboseli, and correcting climate data misprinted in Dunbar (1992*b*: table 3). Predicted feeding and social time are significantly similar to the observed time budgets ($p>0.95$). Moving time becomes non-significant when the Badi moving time data were removed (table 3.18).

Equations d and e (different statistical inclusion criteria for step-wise regression: FIN 2.0; FIN 4.0)

Equation (e), which has more stringent criteria for including variables in step-wise regressions (F-value to enter 4.0), produces more non-significant results (i.e. more similar predicted time budgets), than equations generated from less stringent criteria (F-value to enter 2.0). The moving and resting time equations for (d) and (e) were identical (see table 3.13.a.).

Equations f, g and h (short-term climate; long-term climate; and a mixture of long- and short-term climate data)

The aim of the comparison between equations f, g and h, was to assess the importance of proximity versus duration of climate data. The climate data from the long-term source (Anon 1984), were not very proximate to the field sites in all cases. The weather station data for Mount Assirik, Chololo, Amboseli, Giants Castle and Cape Hope were not extremely close to the geographic location of the baboon field site. Climate data from

study years was much more proximate to the baboon field sites, so should have more accurately reflected the local climate. However, as discussed in chapter 2, the duration of climate records in tropical habitats is particularly important, given the large inter-annual fluctuations in rainfall. The third climate data-set (equation h) was a compromise between duration and proximity. In this database long-term records were used where possible, but only when the weather station was close to the field site, otherwise short-term field site climate data were used.

The moving time equations in (f) (g) and (h) are not very accurate, however upon the omission of the Badi moving time data all become highly predictive, particularly equation (g) (long-term climate: $move_{(no\ Badi\ data)}$ p = >0.80). The inaccuracy of the long-term climate data, in terms of proximity, influences the poor predictability of equations (h). From the three climate databases used, the mixture of long-term and short-term data resulted in the most predictive regression equations. Therefore it would appear that the proximity of the weather station to the baboon field site is most important.

Fisher's test on all time budgets combined

Fisher's test was computed for all four time budgets together, for each regression equation (a to h) (table 3.19). However, time budget categories are not independent tests, which violates the assumption of the chi-squared test. Therefore the statistics presented in table 3.19 should be interpreted with caution. Nevertheless, all four time budgets were analysed together in Dunbar (1992*b*), and the analysis in table 3.19 is a useful comparison.

Table 3.19. Fisher's test for combined probabilities from independent tests of significance. All time budgets analysed together, for each equation (a to h). Non-significant p-values shown in bold.

	Equation							
	A	**B**	**C**	**D**	**E**	**F**	**G**	**H**
χ^2	32.44	58.99	36.23	99.165	34.687	31.98	31.94	22.03
k	2	2	2	3	2	2	2	2
df	32	30	32	32	32	30	32	30
p	**>0.30**	<0.01	**>0.20**	<0.0001	**>0.20**	**>0.30**	**>0.30**	**>0.80**

***a:** Bronikowski & Altmann (1996); **b:** Dunbar (1996); **c:** this thesis; **d:** fin (2.0) fout (1.996); **e:** fin (4.0) fout (4.0); **f:** short-term climate data; **g:** long-term climate data; **h:** mixture of long-term and short-term climate data.

The most predictive equations, are those generated from a mixture of long- and short-term climate (equation h). The least predictive equations were b (Dunbar 1996) and d (F-value to enter 2.0) which produced time budgets significantly different from the observed values. The Dunbar (1992*b*) equations are not reanalysed here, since Fisher's test results were presented in the 1992 publication. Observed values were found to be significantly more similar to the values predicted by the Dunbar (1992*b*) equations than would be expected by chance (χ^2 = 17.88, df = 2, k = 32, p >0.95). Nearly half the χ^2 value was accounted for by the possibly aberrant Badi moving time point (Badi moving time removed: χ^2 = 8.419, df = 30, p>0.995).

3.6.2. Maximum ecologically tolerable group size predicted from different equations

Having assessed the accuracy of the equations (a) to (h) in predicting the time budgets in the subsidiary sample, the next step was to use these equations to model maximum ecologically tolerable group size. The regression equations derived in this chapter (see tables 3.11, 3.13a & b), were to used as inputs in the BASIC model (see section 3.4.2.ii, figure 3.2 and appendix II part 2) to predict maximum ecologically tolerable group sizes. The equations highlighted in bold in appendix II part 2, were replaced by the relevant equations from tables 3.11, 3.13 a & b.

The ecological equations used in the model related the rainfall diversity indices (V (number of months with <50mm rainfall) and Z (Simpson's index of rainfall diversity)) to the model output dimensions; rainfall and temperature (see section 2.4.6)

$$V = 11.4897 - 0.7078(P)+0.0000015(P)^2 \quad (r^2=0.714;\ n = 218)$$

$$Mo50=1.04-0.012(V)-0.003(T) \quad (r^2=0.425,\ n = 218)$$

These ecological equations were used in the models of maximum ecologically tolerable group size in Dunbar (1996) (*Papio* baboons) and Strivastava & Dunbar (1996) (Hanuman langurs).

Different equations for social and resting time were used from those generated in the step-wise regression equations of time budgets. Dunbar (1996) argued that social and resting time were of lower ecological priority than feeding and moving. Feeding and

moving time are dictated more by ecological and demographic constraints, therefore the allocation of time to these categories is beyond the control of the animal. Animals have greater flexibility in their allocation of time to resting and socialising. Therefore resting and social time budgets are likely to reflect compromise values *after* the animals have evaluated what they *ought* to do and the minimum time they should allocate, still leaving enough time for feeding and resting. In marginal habitats, animals may have to compromise so much time on social and resting time that it leads to them being unable to survive in that particular habitat. Resting time in the model was subject to a minimum value of 5% (Dunbar 1992*b*, Dunbar 1996). The primary constraint on resting time was thought to be the need to seek shelter when ambient temperature rose above a critical threshold at midday. The resting time equations in all cases (equations a to h) included an environmental component, which supports this assertion.

The amount of time allocated to socialising, was constrained by the minimum amount of time needed to service relationships (Dunbar 1991). A linear regression set on the old world monkey and ape grooming times, in Dunbar (1991) yielded the following equation (see Dunbar 1996: 42)

$$\ln(S) = -2.275 + 1.32\ln(N) - 0.0445\ln(N)^2$$

($r^2 = 0.997$, n = 13 generic means for Catarrhine primates)

An additional ecological constraint was placed in the model of maximum ecologically tolerable group size. Limiting constraints were placed on *Z* (Simpson's index of rainfall diversity), where there was an upper limit of Z = 0.918 (see section 2.3).

The following tables illustrate the maximum ecologically tolerable group sizes predicted by the model. Maximum ecologically tolerable group sizes (N_{max}), were estimated for temperatures 0 to 35°C, and 100-2900mm rainfall.

Equations a, b and c (Bronikowski & Altmann 1996; Dunbar 1996; this thesis)

The equations presented in Dunbar (1992*b*) were subsequently improved (Dunbar 1996). The difference between the two sets of equations used to generate N_{max} differed primarily in the feeding time equation, where the equation was reversed at 30°C to reflect the

increase in energy consumption above 30°C (Mount 1979). Qualitatively, the results for N_{max} from the Dunbar (1992*b* and 1996) equations both indicate that baboons can only occupy a limited range of habitats. Baboons cannot survive in extremely hot, dry habitats, nor at low temperatures. Above 1500mm rainfall, baboons find it increasingly difficult to sustain groups of any size.

The Bronikowski & Altmann (1996) equations produced group sizes of a similar magnitude to those in tables 3.20 (a & b) above 1300mm rainfall. At higher temperature and rainfall values, group sizes remained relatively high.

The group sizes generated from equation (c) (this thesis), were more similar in magnitude to Dunbar (1996). However, the region 1300 to 2700mm rainfall, across temperatures 15 to 35°C produced fairly stable group sizes. The aim of these equations (c) was to correct data in Dunbar (1992*b*) and incorporate new data from Amboseli. The equation for feeding time was not adjusted for increasing costs above 30°C, and this may account for the continued increase in N_{max} at 35°C.

Equations d and e (different statistical inclusion criteria for step-wise regression: FIN 2.0; FIN 4.0)

Table 3.21 a & b illustrate N_{max} generated from equations (d) and (e) respectively. The data used to compute the regressions in equations (d) and (e) was identical to that in Dunbar (1992*b*). The comparison of the two statistical criteria for inclusion in step-wise regression (F-value to enter 2.0, or 4.0), arose from correspondence with A. Bronikowski (see Bronikowski & Altmann 1996). Using the same database, we appeared to be getting different regression equations which we thought might be due to different statistical criteria used by different computer packages. This analysis illustrates the importance of the statistical inclusion criteria, particularly for small sample sizes. The more stringent criteria (F-value to enter) results in too few variables entering the predictor set. This conclusion is supported by the Fisher's test of combined probabilities, comparing equations (d) and (e) (see above).

Equations f, g and h (short-term climate; long-term climate; and a mixture of long- and short-term climate data)

The predictions of N_{max} support the conclusions from the Fisher's test of combined probabilities, comparing equations f, g and h (see above). The short and long-term climate data produce values for N_{max} at low temperatures. The short-term climate equations do not generate different values for N_{max} at increasing values of rainfall, except at higher temperatures (≥25°C). The values for N_{max} generated from the equations using long-term climate data are the most anomalous. Maximum group sizes of 70 are predicted for the bottom diagonal half of table 3.22 (b). The equations used to predict N_{max} from the long term climate data contain very few predictors (Feeding: *Z*; moving: *N*; resting: *F*). The reduced number of predictor variables appears to affect the accuracy of prediction of N_{max}, compared to those sets of equations with more predictor variables.

The mixed climate data equations (h) generate equations similar to those generated by Dunbar (1996) (table 3.20.b). The Fisher's test of combined probabilities shows that this set of equations (h) most accurately predicts time budgets in the subsidiary sample. The success of the mixed-climate data in predicting time budgets, highlights an issue raised by Bronikowski & Altmann (1996). They pointed out that for sites with high annual rainfall, year to year differences in mean annual rainfall would be slight compared to very low rainfall sites (e.g. Amboseli). Therefore, they would expect little effect of using long-term versus short-term climate data for high rainfall sites. Whereas, for low rainfall sites, such as Amboseli, year to year fluctuations in rainfall would be relatively more exaggerated. Contrary to Bronikowski & Altmann's (1996) suggestion that we should therefore use study-year data (particularly at low-rainfall sites), I would still advocate the use of accurately placed long-term climate data, irrespective of the magnitude and seasonality of mean annual rainfall. Given success of the mixed climate data, proximity of weather stations to baboon field sites should be emphasised, over and above the duration of the climatic records.

Table 3.20. Maximum ecologically tolerable group size from equations in table 3.11

(a) Dunbar (1992*b*)

Rain	Temperature (°C)							
(mm)	**0**	**5**	**10**	**15**	**20**	**25**	**30**	**35**
100	0	0	0	69	151	176	27	0
300	0	0	0	73	156	187	41	0
500	0	0	0	77	160	197	59	0
700	0	0	0	81	164	208	80	0
900	0	0	0	84	166	218	105	0
1100	0	0	0	85	167	228	132	0
1300	0	0	0	83	166	237	162	0
1500	0	0	1	79	161	244	195	0
1700	0	0	1	69	151	248	231	0
1900	0	0	1	51	132	246	268	0
2100	0	0	0	22	96	232	304	0
2300	0	0	0	0	29	188	333	27
2500	0	0	0	0	0	31	305	272
2700	0	0	0	0	0	0	46	419
2900	0	0	0	0	0	0	46	419

(b) Dunbar (1996)

Rain	Temperature (°C)							
(mm)	**0**	**5**	**10**	**15**	**20**	**25**	**30**	**35**
100	0	0	9	23	31	30	22	7
300	0	0	15	39	54	58	52	31
500	0	1	18	48	70	79	79	57
700	0	1	19	52	80	96	101	80
900	0	1	19	53	84	107	119	100
1100	0	0	16	51	84	112	131	114
1300	0	0	12	45	79	109	136	121
1500	0	0	8	35	70	102	131	118
1700	0	0	4	24	56	89	118	105
1900	0	0	2	14	40	71	101	85
2100	0	0	0	7	26	53	81	63
2300	0	0	0	4	16	37	62	44
2500	0	0	0	2	10	26	48	31
2700	0	0	0	1	7	20	39	24
2900	0	0	0	1	6	17	35	21

(c) Bronikowski & Altmann (1996)

Rain	Temperature (°C)							
(mm)	**0**	**5**	**10**	**15**	**20**	**25**	**30**	**35**
100	0	0	10	50	66	62	44	19
300	0	0	3	43	68	71	59	37
500	0	0	0	36	67	77	72	54
700	0	0	0	28	65	82	82	69
900	0	0	0	29	62	84	84	82
1100	0	0	0	33	63	86	86	93
1300	0	0	0	37	69	88	88	103
1500	0	0	1	42	75	95	95	111
1700	0	0	1	46	81	102	102	119
1900	0	0	2	51	87	108	108	126
2100	0	0	3	56	93	114	114	132
2300	0	0	4	59	97	119	119	133
2500	0	0	4	61	99	122	122	139
2700	0	0	4	61	99	122	122	139
2900	0	0	4	59	97	119	119	136

(d) This thesis

Rain	Temperature (°C)							
(mm)	**0**	**5**	**10**	**15**	**20**	**25**	**30**	**35**
100	0	0	19	80	125	156	177	192
300	0	0	4	53	95	124	145	158
500	0	0	0	37	78	107	128	142
700	0	0	0	25	66	96	117	132
900	0	0	0	21	56	87	110	125
1100	0	0	0	20	51	81	104	121
1300	0	0	0	18	50	76	100	117
1500	0	0	0	17	49	75	97	115
1700	0	0	0	17	49	75	95	114
1900	0	0	0	16	48	75	95	112
2100	0	0	0	15	48	74	95	111
2300	0	0	0	15	47	74	94	110
2500	0	0	0	13	45	71	91	107
2700	0	0	0	11	42	67	87	103
2900	0	0	0	9	38	63	82	98

Table 3.21. Maximum ecologically tolerable group size from equations from table 3.13a.
(a) Dunbar (1992*b*) data. Statistical criteria for regression: FIN(2.0) FOUT(1.996)

Rain	Temperature (°C)							
(mm)	**0**	**5**	**10**	**15**	**20**	**25**	**30**	**35**
100	0	0	4	18	50	96	149	201
300	0	0	4	21	57	108	164	219
500	0	0	4	10	55	106	164	221
700	0	0	5	19	52	104	164	225
900	0	0	5	18	45	93	152	212
1100	0	0	5	19	44	85	143	205
1300	0	0	5	20	45	79	134	197
1500	0	0	5	20	46	80	125	187
1700	0	0	5	20	45	80	118	177
1900	0	0	5	19	44	78	116	166
2100	0	0	5	17	41	73	110	153
2300	0	0	4	17	41	73	111	150
2500	0	0	4	17	41	73	110	150
2700	0	0	4	18	42	75	113	152
2900	0	0	5	18	43	77	115	154

(b) Dunbar (1992*b*) data. Statistical criteria for regression: FIN(4.0) FOUT(4.0)

Rain	Temperature (°C)							
(mm)	**0**	**5**	**10**	**15**	**20**	**25**	**30**	**35**
100	0	0	0	0	0	0	0	0
300	0	25	25	25	25	25	25	25
500	113	113	113	113	113	113	113	113
700	178	178	178	178	178	178	178	178
900	233	233	233	233	233	233	233	233
1100	280	280	280	280	280	280	280	280
1300	321	321	321	321	321	321	321	321
1500	359	369	359	359	359	359	359	359
1700	392	392	392	392	392	392	392	392
1900	420	420	420	420	420	420	420	420
2100	444	444	444	444	444	444	444	444
2300	463	463	463	463	463	463	463	463
2500	476	476	476	476	476	476	476	476
2700	483	483	483	483	483	483	483	483
2900	483	483	483	483	483	483	483	483

Table 3.22. Maximum ecologically tolerable group size from equations from table 3.13a.

(a) Short-term climate data.

Rain	Temperature (°C)							
(mm)	**0**	**5**	**10**	**15**	**20**	**25**	**30**	**35**
100	96	214	231	240	246	246	210	0
300	96	214	231	240	246	218	152	0
500	96	214	231	240	246	213	141	0
700	96	214	231	240	246	216	149	0
900	96	214	231	240	246	223	164	0
1100	96	214	231	240	246	230	179	0
1300	96	214	231	240	246	237	194	0
1500	96	214	231	240	246	237	207	0
1700	96	214	231	240	246	239	216	159
1900	96	214	231	240	246	241	219	175
2100	96	214	231	240	246	242	221	187
2300	96	214	231	240	246	243	223	194
2500	96	214	231	240	246	243	222	192
2700	96	214	231	240	246	240	217	185
2900	96	214	231	240	246	235	209	172

(b) Long-term data

Rain	Temperature (°C)							
(mm)	**0**	**5**	**10**	**15**	**20**	**25**	**30**	**35**
100	75	84	92	100	106	112	116	119
300	70	73	82	91	98	105	111	115
500	70	70	72	82	90	98	105	110
700	70	70	70	73	82	90	98	105
900	70	70	70	70	74	83	91	99
1100	70	70	70	70	70	76	85	93
1300	70	70	70	70	70	70	79	87
1500	70	70	70	70	70	70	73	82
1700	70	70	70	70	70	70	70	78
1900	70	70	70	70	70	70	70	74
2100	70	70	70	70	70	70	70	72
2300	70	70	70	70	70	70	70	70
2500	70	70	70	70	70	70	70	70
2700	70	70	70	70	70	70	70	70
2900	70	70	70	70	70	70	70	70

(c) Mixed climate data

Rain	Temperature (°C)							
(mm)	**0**	**5**	**10**	**15**	**20**	**25**	**30**	**35**
100	0	9	34	48	56	61	65	67
300	0	11	39	55	64	71	75	78
500	0	14	44	62	73	80	85	89
700	0	17	51	69	81	90	96	100
900	0	21	57	77	90	99	106	111
1100	0	25	64	85	98	108	116	122
1300	0	29	70	92	107	117	125	132
1500	0	32	76	100	115	126	134	142
1700	0	36	81	106	123	134	143	151
1900	0	39	86	112	129	141	151	158
2100	0	41	90	117	135	147	157	165
2300	0	43	93	121	139	152	162	169
2500	0	44	95	123	141	154	164	172
2700	0	44	95	123	141	154	164	172
2900	0	43	93	121	139	152	162	169

3.7. CONCLUSION

In this chapter existing models of baboon socioecology were reviewed and extended. The principal aim of these models was to quantitatively examine the relationship between environmental and demographic variables. Baboon time budgets were used to develop functional equations of the relationship between environmental and behavioural (time budget) data. The environmental and behavioural data used as inputs for these models was carefully reviewed in the light of recent criticisms (Bronikowski & Altmann 1996; Bronikowski & Webb 1996).

The statistical methods for step-wise regression were carefully reviewed, particularly with respect to the relatively small samples sizes of data available. When interpreting the multiple regression equations, care was taken not to over-interpret the data. Whilst regression equations allowed good predictability, they do not infer *causation*. The data were carefully screened before analysis, to avoid violating the assumptions of stepwise regression. In response to the criticisms of Bronikowski & Altmann (1996), that stepwise regression should be used with caution, particularly with observational data, several points can be raised. Stepwise regression does not always choose the same "important" explanatory variables between analyses, therefore a balance between univariate and multivariate analyses was advocated. In this chapter, the correlation matrices were carefully examined before constructing multiple regression equation, to avoid the confounding factor of inter-correlating variables (collinearity). Natural logarithm transformations were sufficient to normalise data, and enable comparison between the newly generated equations, and those in Dunbar (1992*b*; 1996) and Bronikowski & Altmann (1996).

Climate data from three sources was carefully collated from the literature: long-term data (Anon 1984); study year data (government publications); study year data (field site publications). A compromise data set, of long and short-term climate data, emphasising proximity of weather data to the field site was also compiled. The long-term climate data base had a greater number of meteorological variables available. However, as shown in chapter 2 (fig. 2.12), habitats can be economically characterised

by three environmental variables. This was supported by the comparison of the initial comparisons between environmental and behavioural variables. Principal components analyses were performed on the small samples of environmental variables (n=13) from the four sources of climate data (Dunbar 1992*b*; study year climate; long-term climate; mixture of short- and long-term climate). The baboon field sites revealed similar dimensions of climatic variables to those found in chapter 2. The functional equations between behavioural and environmental variables for the four climatic sources were broadly similar. This highlighted the robusticity of the equations in relation to the proximity and time scale of the climatic data. One of the criteria of multiple regression equations is that they should be biologically plausible, which is met by the equations in this chapter.

Having compared the multiple regression equations generated from the different climate data, and corrected time budget data, the equations were used to predict time budgets from a subsidiary sample (n = 4). When corrections of time budget data, and addition of new data were made to the original 1992 database (equations a and c), the equations more accurately predicted the time budgets in the subsidiary sample. The moving time data for Badi was thought to be underestimated (Dunbar & Nathan 1972), and when removed resulted in even greater accuracy of prediction of the time budgets in the subsidiary sample.

When comparing the different statistical criteria for inclusion for stepwise regression, the more stringent criteria resulted in too few predictor variables entering the multiple regression equation to sufficiently explain the variance in the dependent variable. This was particularly reflected when these equations were used to predict maximum ecologically tolerable group sizes. These equations were the least successful in predicting maximum ecologically tolerable group sizes in the range of temperatures and rainfalls that would be expected. For example, the equations did not distinguish different group sizes for different rainfall values.

When the three climate data sources were compared (short-term, long-term and mixed), the mixture of long- and short-term data were most accurate at predicting time

budgets in the subsidiary sample. It is assumed that long-term climatic conditions best predict the vegetation structure of the habitat. The vegetation available to animals in any one study year will have been the product of the previous years climate. Therefore we would expect animals to adjust their time budgets to the resources available in the study year, which will in turn have been influenced by longer term climatic conditions. From this analysis, it appears that the weather stations for the long-term climate data were too far away from the field sites, to represent climate there. Therefore, proximity of data seems important over and above the duration of the climate data record. This finding emphasises the importance for future comparative work, of sufficient continuous long-term climate data from primate field sites. The significance of site-specific climate data was emphasised by a study of Namibian baboons (Cowlishaw 1993). Baboons would not normally be expected to survive in such desert conditions, however in this study there was a local water resource sufficient to sustain the population. The amount, or quality of standing water may be important in influencing whether or not an animal can survive in a given habitat. Whenever permanent water provides sufficient vegetation at the micro-habitat level, baboons can survive in extreme conditions that would not normally support them. As yet, no method has been devised to assess the impact of the amount of standing water, except by increasing the rainfall value. In addition to ground water, the distance to water resources could be important in allowing animals to survive in otherwise uninhabitable areas.

The analyses in this chapter have shown that we can define a set of equations that constrain quite tightly the range of group sizes that a given primate species can occupy. This chapter has focused primarily on relative importance of the data used as inputs in such socio-ecological models. Despite the variable climate data, the equations remain relatively robust in their predictions of maximum ecologically tolerable group size.

In the following chapter I shall extend the systems models approach to modelling maximum ecologically tolerable group sizes, to the chimpanzees. The extension of the model to the chimpanzees aims to verify further the general applicability of this modelling approach to other primate taxa.

CHAPTER 4. CHIMPANZEE SOCIOECOLOGY

CHAPTER 4. CHIMPANZEE SOCIOECOLOGY

4.1. INTRODUCTION

The previous chapter critically examined previous models of baboon socioecology. Modelling methodology and data inputs were systematically analysed. This chapter will build on that knowledge to develop a systems model of chimpanzee socioecology. Chimpanzees are most frequently used as referential models for the early hominids (see 1.2.1.ii, iii). The models presented in this thesis are attempts to develop further the conceptual modelling approach advocated by Tooby & deVore (1987) (see 1.1.2.iii). Therefore any potential model species should be viewed in terms of its specific behavioural adaptations to ecological circumstances. This is in direct contrast to selecting a model species as a direct referent (see 1.2.1.i, ii). I wish to first distinguish the chimpanzee model to be presented in this chapter from existing chimpanzee models of early hominid behaviour. The existing chimpanzee models exist as either direct referents (e.g. Tanner 1981; 1987; Susman 1987) or phylogenetic analogues (e.g. Wrangham 1987), or modifications of either method (see 1.2.1).

Nevertheless whilst chimpanzees in this chapter will be used in conceptual models, there are aspects of their selection as model species that have reasoning grounded more in referential models (reviewed in Moore 1996). If the aim is to extrapolate from models on extant primates to the early hominids, the model species should have *some* dimensions of similarity. Therefore it is important to identify the dimensions on which the model species differs or is similar to the early hominids. The early hominids, and the last common ancestor (LCA), are thought to be of similar size, encephalisation, habitat and diet to the extant chimpanzees. Conceptual models start from the premise that the same selection pressures that act on animals in the present also acted in the past. There are important differences between the early hominids and chimpanzees, notably sexual dimorphism. The australopithecines were highly sexually dimorphic (Kelley 1993; Kimbel *et al.* 1994). The conceptual modelling approach (*sensu* Tooby & DeVore 1987) can accommodate the difference in sexual dimorphism, whereas

referential models (e.g. Zihlman 1984) cannot. Referential models use chimpanzees on homologous grounds (similarity due to common descent) and molecular evidence supports this (see 4.3.1.). Baboons are often cited in referential models on analogous grounds (similarity due to common adaptation) for sharing a similar ecological niche to the early hominids. However this reasoning may be further questioned by recent palaeoecological evidence for the early hominid sites. The exact habitat type for the early hominids may range from woodland (e.g. Sikes 1994); to sub-tropical forest (e.g. Kingston *et al.* 1994) (see 1.4.1.ii.).

The advantage of systems models is that they quantitatively examine the relationship between the components of a system, in this case a social system. Additionally, systems models are capable of reproducing the fine-tuned responses of animals to the different variables that influence behaviour. The cost-benefit approach to define an animals ecologically tolerable zone (outlined in chapter 2) defines the multi-dimensional space an animal occupies. This approach has greater flexibility than conventional referential models using chimpanzees.

In the following chapter, I shall develop a systems model of chimpanzee ecology analogous to that for the baboons in the previous chapter. Behavioural data come from the published literature on populations of wild chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*). Environmental data come from both the chimpanzee literature and climatic data from nearby weather stations.

4.2. CHIMPANZEE CLIMATE DATA

4.2.1. Introduction

The systems models of baboon socioecology (chapter 2) demonstrated that functional equations relating environmental and behavioural variables from climatic data closely situated to the field site were most predictive. Long-term climate was still thought to be preferable, so long as the weather station was close to the study site. To conduct a similar comparative analysis of chimpanzee socioecology long-term climate data were

Weather stations were selected as close as possible to the geographic locations of chimpanzee and bonobo field sites. The duration of chimpanzee studies varies from continuous and long-term, to intermittent and short-term (see appendix III, part 1). Therefore the quality of climate data recorded from field sites during the period of study will differ accordingly. Rainfall in the monsoon zones in Africa show enormous fluctuations from year to year. Consequently short-term records should be avoided, or reassessed in comparison with long-term records from surrounding meteorological stations. Specifically with reference to the Mount Assirik site, McGrew *et al.* (1981) cited mean a rainfall of 954mm for the period 1976-79. However, by interpolation from surrounding areas, a value of 1162mm to 1240mm was thought more accurate (Kortlandt 1983*a*, *b*). In addition to the geographic proximity of weather stations altitude is an important factor. Whilst temperature primarily varies with altitude (see chapter 2, table 2.12), rainfall at high altitudes may increase due to orographic effects. The first attempt to compare the behavioural ecology of chimpanzees between field sites (McGrew *et al.* 1981), was criticised by Kortlandt (1983*b*) (but see reply McGrew *et al.* 1983), for it's too heavy a reliance on field site climate data (short-term and prone to inaccuracy due to high inter-annual fluctuations). Comparative studies of chimpanzees at different field sites, characterising habitat types by climatic variables have been conducted (Baldwin *et al.* 1981; Baldwin *et al.* 1982; McBeath & McGrew 1982; McGrew 1983; McGrew *et al.* 1981), however the meteorological data used were short-term study site data. In this study I shall extend these analyses by supplementing study year climate data with long-term data from nearby weather stations.

The classification of the ecological contexts of chimpanzees has been discussed in the literature in relation to climate. McGrew *et al.* (1981) classified Niokolo-Koba park as the "driest site at which chimpanzees have been studied, in terms of annual rainfall, proportion of dry months, and the number of rainy days" (McGrew *et al.* 1981: 227). However, in reply Kortlandt (1983*b*) pointed out that not all ecological parameters had been considered, for example; geography, topography, climate, vegetation, soil conditions, food and competitors etc. Nevertheless, to conduct comparative analyses of

chimpanzee populations, there needs to be sufficient *comparable* detailed ecological data. A recent compilation of data, experimentally released on the internet by J. Moore (Anthropology Dept. University of California at San Diego), and in the published literature (Wamba: Idani *et al.* 1994; Ugalla (Tongwe): Moore 1994; Nouabale-Ndoki National Park: Moutsambote *et al.* 1994; Lopé: Tutin *et al.* 1994; Kahuzi-Biega National Park: Yamoto *et al.* 1994) attempted to redress this lack of comparable detailed ecological detail from the chimpanzee field sites. However, these databases only contained data on plant food species eaten, plant part eaten and habitat occupied. These data were not useful for quantitative analyses, whereas data on the frequency of plants eaten and the energetic/nutritional value of the plant, for example, would have been. Nevertheless, this information was useful qualitatively, and is useful in comparing the diets of chimpanzees in different parts of Africa. For example, the bonobo field site data (Idani *et al.* 1994) listed 515 species of plants belonging to 64 families occurring at Wamba since 1974. This database provided more quantitative information, presenting data from a belt transect 4m × 4150m. Three separate transects in the major forest types; primary, secondary and swamp forest were conducted, providing data on the total basal area and density of tree stems. This additional information on terrestrial herbaceous vegetation (THV) suggested stable rich food sources, suggested to be responsible for sustaining the large party sizes of bonobos at Wamba (Idani *et al.* 1994).

4.2.2. Sources of chimpanzee climate data.

As with the baboon climate data (section 3.5.1.), two criteria were used when selecting climate data sources and weather stations: (1) the proximity of weather stations to chimpanzee field sites, and (2) the time scale of the records (whether year to year, or long term average data were given). The years for which environmental data were required for the chimpanzee field sites are listed in table appendix III part 1 (refer to figure 4.12.b. for a map of the locations of the chimpanzee field sites).

Five sources of climate data were used;

1. Long term data (Anon 1984)
2. Long term data (Nicholson *et al.* 1988)
3. Long term data (Hulme 1993)
4. Study year data (Government publications)
5. Long term and study year data (Publications on chimpanzee field sites)

The location of the climate data source in relation to the field sites for each of the sources of data are shown in the following tables.

1. Climate data source: Anon (1984), H.M.S.O. compilation.

Table 4.1. illustrates the location of each weather station and its proximity to each chimpanzee field site.

Table 4.1. Nearest weather station to the chimpanzee and bonobo field sites (Anon 1984).

Site name	Country	Map reference	Nearest H.M.S.O site	H.M.S.O. site map reference
Pan troglodytes				
Mount Assirik	Senegal	12°53'N 12°00'W	Ziuuichor	12°35'N 16°16'W
Budongo	Uganda	01°45'N 31°28'E	Anasindi	01°43'E 31°43'E
Kibale	Uganda	00°34'N 30°21'E	Fort Portal	00°40'N 30°17'E
		00°30'N 30°25'E	Entebbe	00°03'N 32°27'E
Gombe	Tanzania	04°40'S 29°38'E	Kigoma	04°53'S 29°38'E
Mahale	Tanzania	06°07'S 29°30-55'E	Dodoma	06°10'S 35°46'E
Kasakati	Tanzania	05°23'S 29°55'E	*	*
Mount Okorobiko	Equatorial Guinea	09°53'E 01°29'N	Iringa	07°41'S 35°45'E
Bossou	Guinea	07°39'N 08°30'W	**	**
Lopé	Gabon	00°10'S 11°35'E	**	**
Taï Forest	Ivory Coast	05°52'N 07°28'W	**	**
Pan paniscus				
Wamba	Zaire	00°01'N 22°34'E	**	**
Lomako	Zaire	00°51'N 21°05'E	*	*
Yalosidi	Zaire	02°19'S 23°15'E	Tabou	04°25'N 07°22'W

* No HMSO published weather stations any where near the study site
** No HMSO published records for the entire country.

The data available from each of the weather stations was tabulated by month for an average of 30 years variables: temperature (maximum, minimum, daily mean, absolute maximum and absolute minimum); relative humidity (%) for a.m., midday and p.m. Wind speed and hours of sunshine were given in some, but not all weather station entries. Of the three main bonobo field sites (Wamba, Lomako and Yalosidi), only

Yalosidi had a weather station relatively close to it (Tabou). However, Tabou is not very proximate to Yalosidi. Similarly, Iringa is not very close to the field site its data represents (Mount Okorobiko). The chimpanzee sites in Senegal, Uganda and Tanzania had data from quite proximate weather stations. This is a consequence of there being more weather stations in those countries, and therefore a higher probability of there being a station proximate to one of the field sites.

2. Climate data source: Nicholson et al. (1988).

The location of the weather stations in relation to the field sites, number of years data, and total years of data are listed in table 4.2.

The weather stations published in Nicholson *et al.* (1988) were extremely close to the chimpanzee field sites. However, only rainfall data, not temperature data were available. The rainfall data is published month by month enabling rainfall seasonality indices to be computed. The mean rainfall values, and rainfall diversity are tabulated in table 4.3. The dataset was then subdivided into data for chimpanzee and bonobo field sites (chimpanzees figures 4.1.a & b; bonobos figure 4.1.c.). Rainfall for the chimpanzees was both unimodal (Mt. Assirik, Bossou) and bimodal (Gombe, Kasakati, Kibale, Taï Forest) in distribution. The seasonality at Budongo is relatively bimodal, the second peak in rainfall is similar in September and November. The absolute maximum rainfall is higher in September, versus October for Budongo. The bonobo field sites are geographically close together, consequently the rainfall mean and distribution is very similar (bimodal, peaking in April and October: see fig. 4.2. a & b.).

3. Chimpanzee climate source: Hulme (1993).

The Hulme database (CRU0092.DAT: Hulme 1993) was useful as a broad indicator of climate in the region of the chimpanzee sites. The Hulme database is a gridded dataset, and only has values for rainfall, therefore only rainfall and indices of rainfall seasonality could be computed from this dataset. The grids were at a resolution of 2.5° latitude and 3.75° longitude, and are those for the north westerly corner of the grid. Data were given

yearly for on average 60 years, month by month. These data were useful in assessing the degree to which individual study year data from chimpanzee publications was representative of the long-term climate in that region. Comparisons could be made by analysing sub-sets of years from the Hulme (1993) record for comparison with short-term records. Table 4.4. lists rainfall data by country, for mean values from several stations. Figure 4.3.a. illustrates the data from sites with a unimodal distribution of rainfall, figure 4.3.b. those sites with a bimodal rainfall distribution pattern.

Table 4.2. Nearest weather stations to each chimpanzee and bonobo field site: Data from Nicholson *et al.* (1988).

Field site			Weather Station					
site	country	grid reference	weather station	grid reference	Altitude (m)	Data first	Data last	Total years data
Pan troglodytes								
Mount Assirik	Senegal	12°53'N 12°40'W	Kolda	12°53'N 14°58'W	35	1922	1979	58
Bossou	Guinea	07°39'N 08°30'W	Beyla	08°41'N 08°39'W	695	1921	1962	42
Budongo	Uganda	01°45'N 31°28'E	Butaba	01°50'N 31°20'E	619	1904	1973	64
Gombe	Tanzania	04°40'S 29°38'E	Kigoma	04°53'S 29°37'E	885	1922	1982	60
Kasakati	Tanzania	05°24'S 29°55'E	Uvinza	05°07'S 30°22'E	991	1928	1982	55
Kibale	Uganda	00°34'N 30°21'E	Mbarara	00°37'N 30°39'E	1443	1912	1983	70
			Bukalasa	00°43N 32°31'E	1128	1965	1968	3
Lopé	Gabon	00°10'S 11°35'E	Fougamu	01°13'S 10°35'E	75	1950	1979	30
Lopé	Gabon	00°10'S 11°35'E	Ndjole	00°11'S 10°40'E	47	1903	1970	27
Mahale	Tanzania	*	*	*	*	*	*	*
Mt. Okorobiko	Tanzania	*	*	*	*	*	*	*
Taï Forest	Ivory Coast	05°52'N 07°28'W	Soubre	04°49'N 06°16'W	250	1940	1979	40
Pan paniscus								
Lomako	Zaire	00°51'N 21°50'E	Yangambi	00°53'N 24°31'E	491	1912	1984	73
Lake Tumba	Zaire	00°55'S 18°00'E	Mondombe	00°55'S 22°42'E	450	1932	1959	24
Yalosidi	Zaire	02°19'S 23°15'E	Tshibinda	02°19'S 28°45'E	2055	1927	1949	20
Wamba	Zaire	00°01'N 22°34'E	Befori	00°05'N 22°18'E	400	1937	1959	21

* No nearest weather station for that site.

Table 4.3. Climate data nearest to chimpanzee sites. Climate data from Nicholson *et al.* (1988).

Weather station	Nearest chimpanzee field site	J	F	M	A	M	J	J	A	S	O	N	D	Total	Mean	SD	Z	Mo50	minP	maxP	DIV	Rain fall Modality	Peak months
Beyla	Bossou	11	38	113	153	185	222	244	247	281	177	81	27	1779	148.25	93.24	0.886	3	11	281	0.806	1	Sep
Soubre	Tai Forest	31	61	131	153	169	224	110	100	213	176	114	52	1534	127.83	61.82	0.899	1	31	224	0.674	2	May, Sep
Kolda	Mount Assirik	0	0	0	0	17	131	255	367	297	118	9	0	1194	99.50	135.037	0.776	7	0	367	1.449	1	Aug
Kigoma	Gombe	123	119	146	156	54	7	3	2	19	51	134	145	959	79.92	62.68	0.870	4	2	156	0.924	2	Apr, Nov
Uvinza	Ugalla	127	131	153	149	37	2	1	2	15	50	148	169	984	82.00	69.27	0.862	5	1	169	0.967	2	Apr, Nov
Buttaba	Budongo	14	30	59	100	91	52	64	81	74	81	70	29	745	62.08	26.53	0.903	2	14	100	0.605	2	Apr, Aug
Mbarara	Kibale	47	62	96	126	80	26	22	61	100	110	120	73	923	76.92	34.72	0.901	3	22	126	0.591	2	Apr, Nov
Befori	Wamba	116	132	195	189	181	147	174	222	241	260	205	149	2211	184.25	43.78	0.912	0	116	260	0.409	2	Mar, Oct
Mondombe	Lake Tumba	117	122	174	176	141	126	141	182	202	234	239	161	2015	167.92	41.38	0.912	0	117	239	0.373	2	Apr, Nov
Tshibinda	Yalosidi	167	181	202	230	176	60	27	63	136	219	208	200	1869	155.75	68.92	0.902	1	27	230	0.590	2	Apr, Nov
Yangambi	Lomako	75	87	151	161	158	112	135	153	193	222	189	102	1738	144.83	44.72	0.909	0	75	222	0.464	2	Apri, Oct

Site = Weather station site (see table 4.2. for grid reference, and years of data), nearest chimpanzee field site in brackets; **total** = total mean annual rainfall (mm). **mean** = mean annual rainfall (mm); **SD** = standard deviation of monthly rainfall (mm); **Z** = Simpson's index of rainfall diversity (see table 2.2. for formula); **Mo50** = the number of months with <50mm rainfall; **minP** = minimum mean monthly rainfall (mm); **maxP** = maximum mean monthly rainfall; **DIV** = rainfall diversity index (see section 2.2.5.).

Figure 4.2.a. Maximum, minimum and mean rainfall at chimpanzee field sites

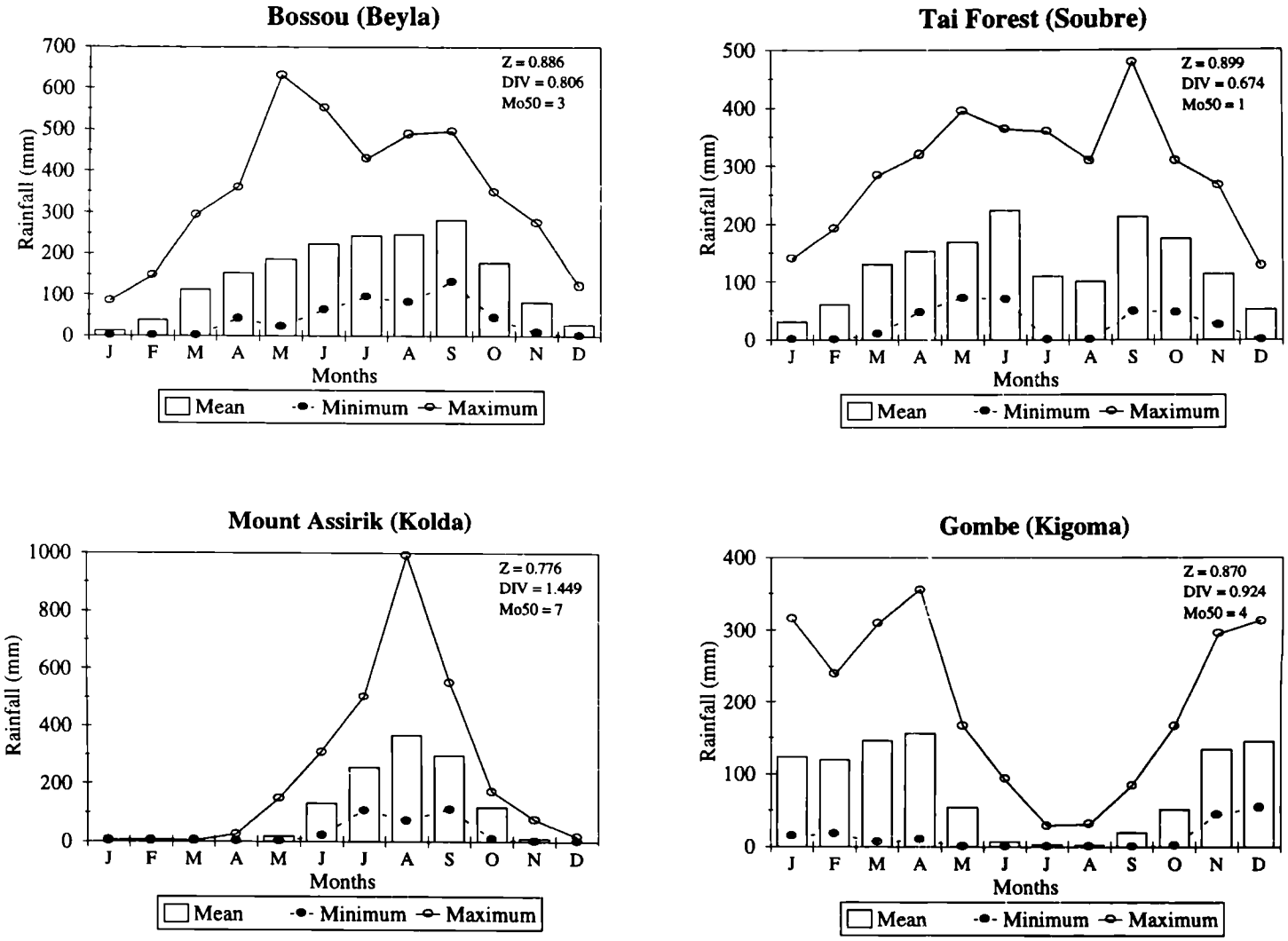


Figure 4.1.b. Maximum, minimum and mean rainfall at chimpanzee field sites

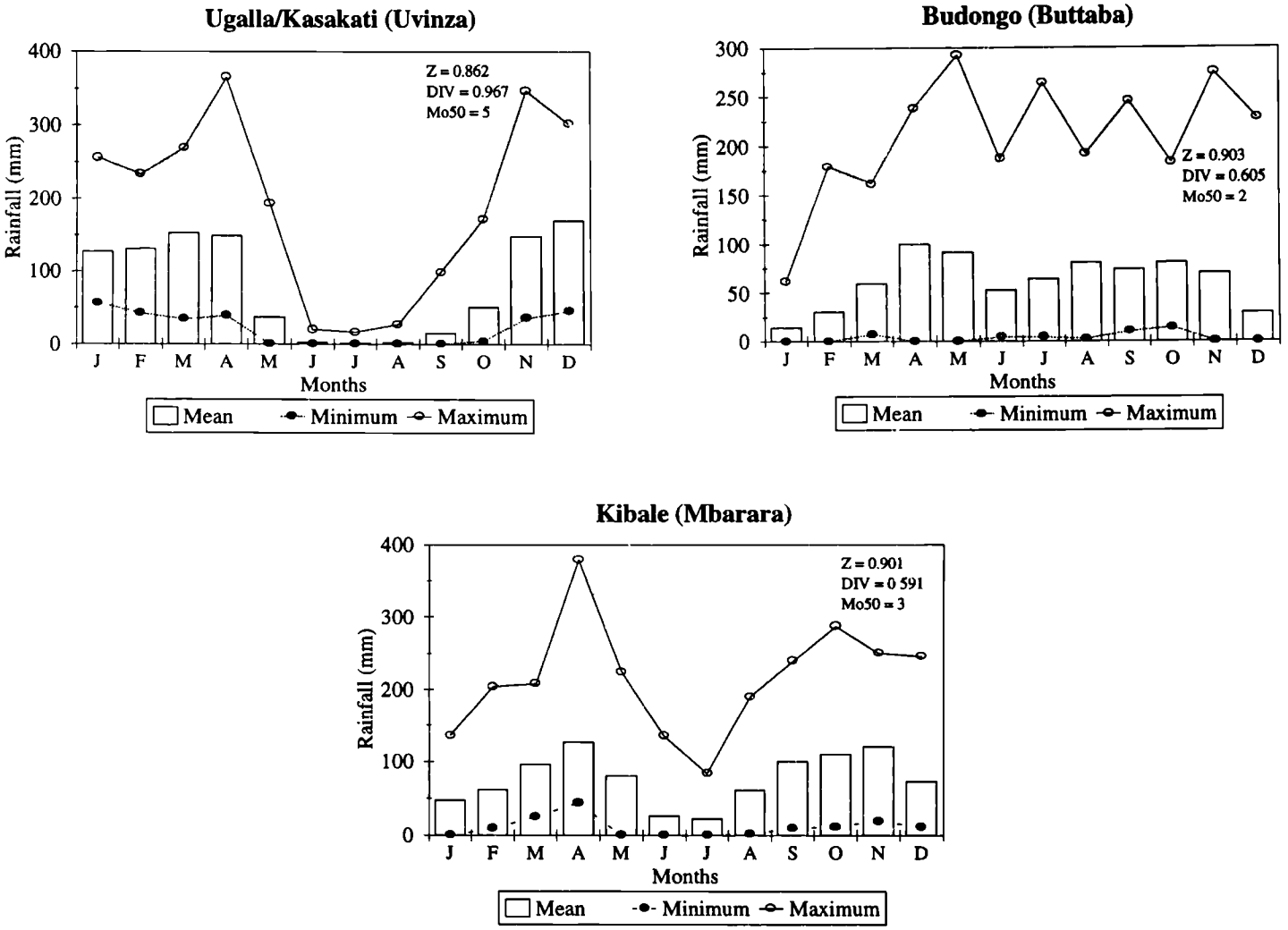


Figure 4.1.c. Maximum, minimum and mean rainfall at chimpanzee field sites

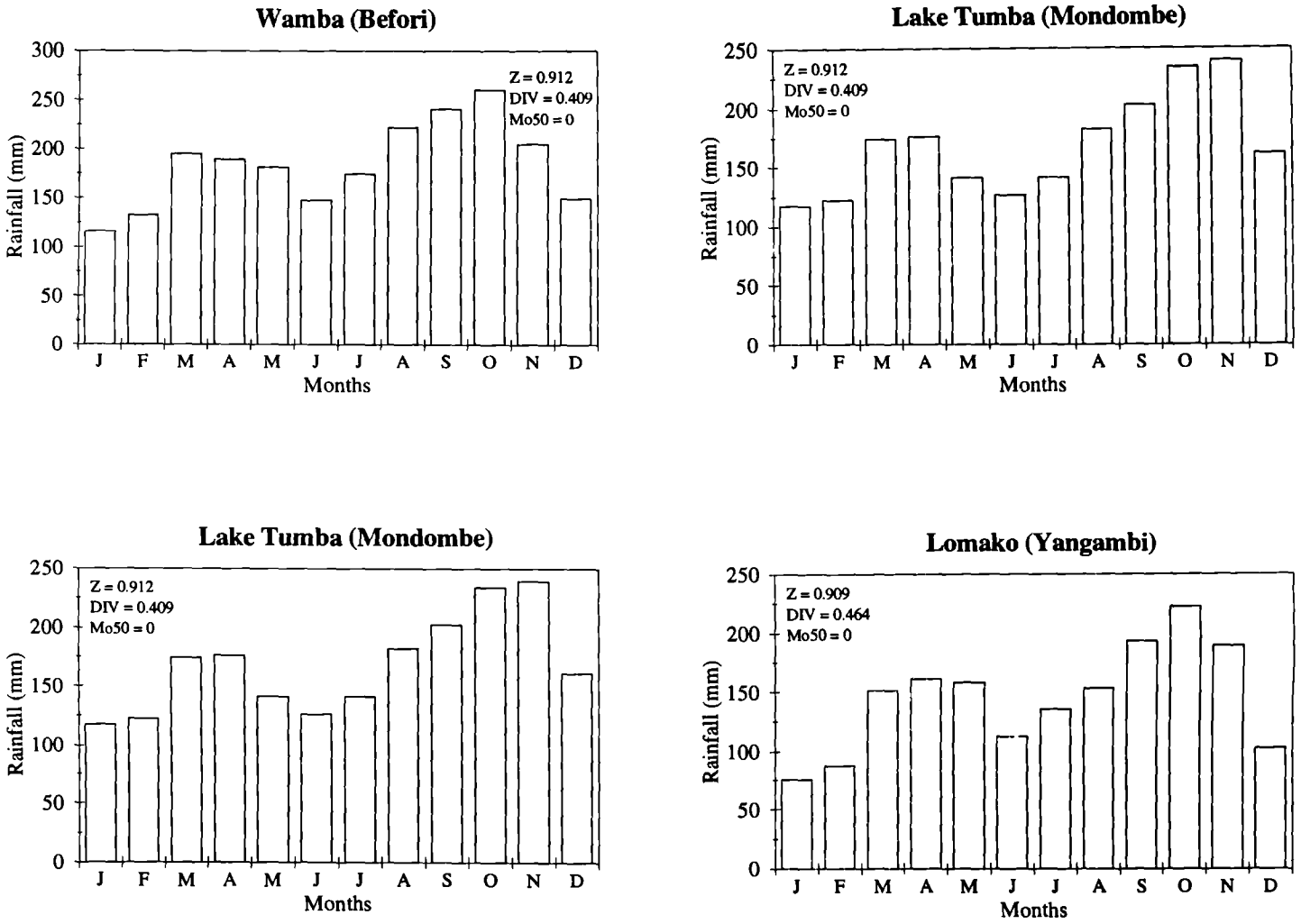


Figure 4.2.a. Mean rainfall for bonobo field sites.

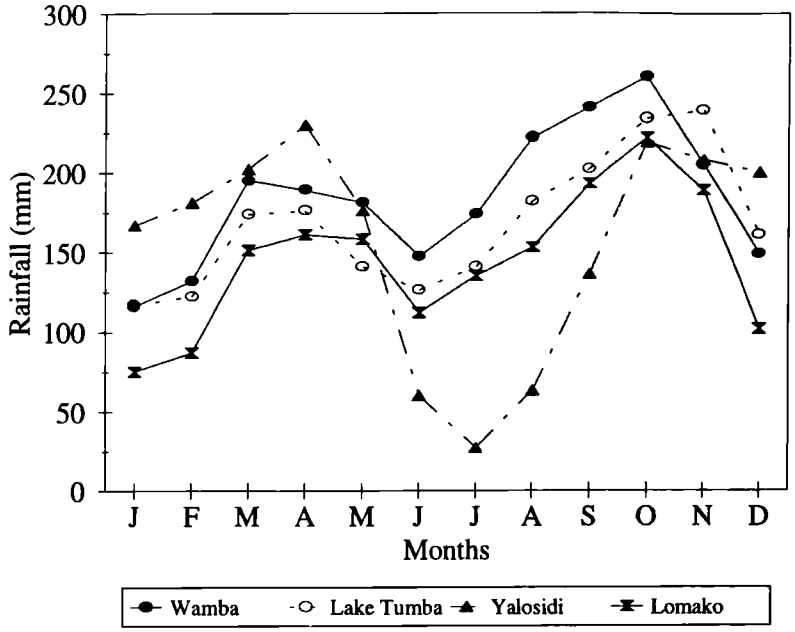


Figure 4.2.b. Mean rainfall for chimpanzee field sites.

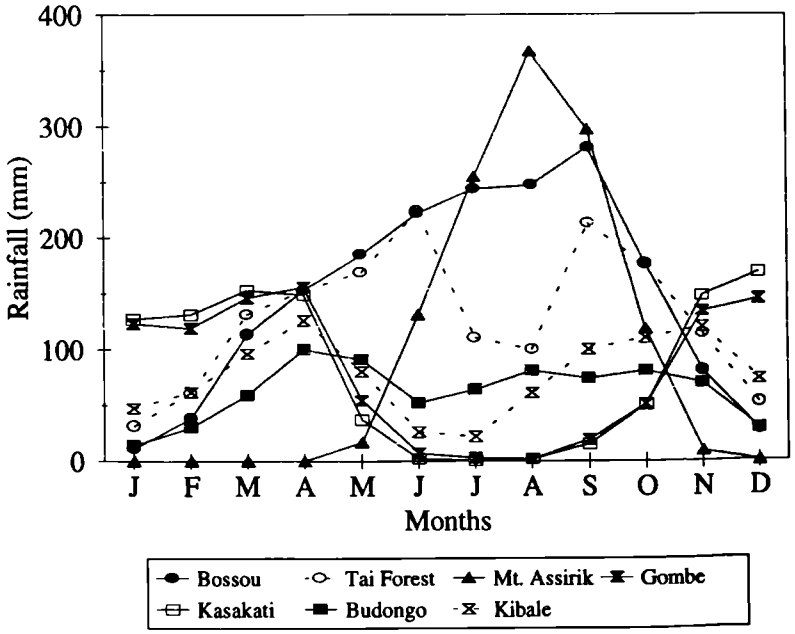


Table 4.4. Mean monthly rainfall by country for those rainfall sites closest to chimpanzee sites, from Hulme (1993).

Country Mean	N	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total	Rainfall Modality *	Peak rainfall month
Guinea	2	1.41	19.86	14.16	43.43	126.81	230.58	335.92	436.80	338.75	201.88	41.24	5.21	1796.04	1	Aug
Angola	6	82.60	85.04	133.03	111.55	22.25	1.00	0.75	6.16	19.59	50.75	92.29	92.39	697.38	2	Mar)
Cameroon	4	42.07	61.71	142.41	177.98	216.44	191.46	179.79	206.97	290.84	309.65	133.46	50.21	2002.97	2	May, Oct
C. Afr. Republic	6	11.46	24.72	80.51	120.67	173.35	183.89	196.29	232.45	228.02	205.89	53.56	14.68	1525.48	1	Aug
Congo	3	133.76	145.50	183.22	173.78	131.80	52.29	48.02	60.23	81.71	143.10	198.96	341.58	1753.24	2	Mar
Gabon	4	200.57	200.56	253.04	237.99	180.29	29.44	3.88	15.48	101.09	319.50	352.36	214.75	2108.93	2	Mar
Malawi	6	246.87	226.37	247.58	121.66	31.87	14.89	11.93	8.08	6.86	22.50	80.88	210.50	1230.00	2	Mar
Tanzania	7	114.20	106.35	139.55	169.42	73.23	13.91	9.63	9.89	16.04	35.08	93.03	135.50	915.84	2	Apr
Uganda	4	48.78	69.28	113.91	166.02	144.34	72.12	71.88	103.65	113.08	121.02	111.22	79.34	1214.63	2	Apr
Zaire	3	125.77	118.97	162.05	179.88	98.07	45.87	50.09	74.65	128.37	181.32	188.90	146.73	1489.50	2	Apr
Ghana	4	23.99	44.95	97.65	127.99	218.76	304.83	154.01	93.36	135.43	152.28	85.52	37.19	1480.17	1	Jun
Guinea Bissau	1	0.55	1.04	0.30	0.33	22.05	188.62	499.36	645.42	409.49	187.28	22.63	68.70	2001.28	1	Aug
Liberia	3	12.27	23.00	48.98	64.16	120.41	246.73	326.68	369.39	272.46	169.78	183.55	380.44	2912.19	2	Aug, Dec
Mali	8	0.44	0.20	0.87	4.26	15.41	40.36	99.76	136.58	71.50	16.08	1.28	0.53	392.76	1	Aug
Nigeria	9	6.39	11.72	36.36	69.39	119.36	162.36	224.21	240.48	209.63	94.67	19.83	6.02	1202.29	1	Aug
Senegal	2	0.46	0.85	0.26	1.44	15.38	95.54	199.24	315.88	223.67	76.40	5.90	1.93	938.70	1	Aug
Sierra Leone	2	10.65	17.84	57.80	121.38	226.20	339.48	509.64	526.01	415.48	259.99	321.59	594.03	2856.51	2	Aug, Dec
Sudan	21	3.52	4.67	12.40	29.47	56.18	75.23	109.62	127.07	86.82	51.07	16.21	5.43	578.11	1	Aug
Mean	95	59.21	64.59	95.78	106.71	110.68	127.14	168.37	200.48	174.93	144.35	111.25	132.51	1495.99	1	Aug

n = the number of gridded data-sets comprising the mean; * Modality = modality of rainfall; 1 = unimodal; 2 = bimodal. Month(s) in brackets indicate month(s) of peak rainfall.

Figure 4.3.a. Rainfall sites with a unimodal distribution.

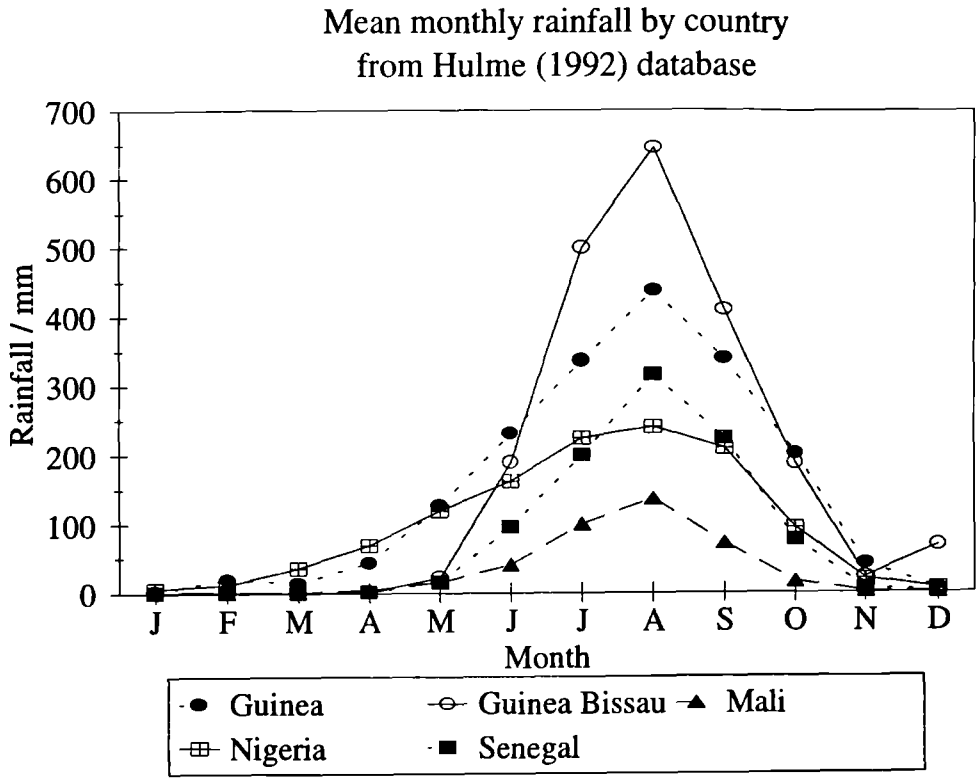
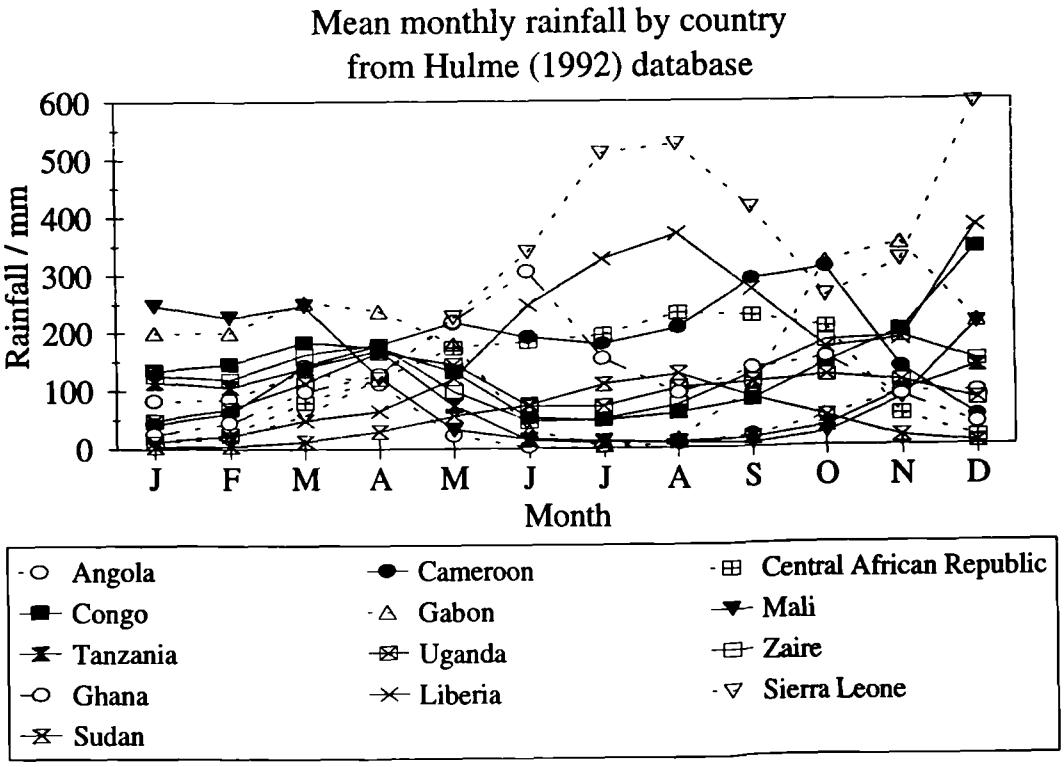


Figure 4.3.b. Rainfall sites with a bimodal distribution.



4. Study year data: Government publications.

Compilations of climate data published by individual country's meteorological departments were available for selected years from the Meteorological Office Library (Bracknell, Berkshire, U.K). Table 4.5. tabulates the relevant weather stations for the chimpanzee sites listed. Data were scarce, and therefore accurately placed sites were only available from three chimpanzee sites. There were no government published records for Zaire available, and therefore no data for the bonobo field sites. The proximity of the weather stations to chimpanzee field sites was very close in all cases. However, the database was limited by the number of years data available. The library only stocked selected issues of the following publications, and not for consecutive years.

Table 4.5. Chimpanzee and bonobo sites with government published data (for the respective country).

Country	Weather station	Map reference	Years of data	Chimpanzee Field site	Map reference
Uganda	Bugusege	1°09'N 34°16'E	1964	Budongo	1°45'N 12°46'W
	Arapai	1°47'N 33°38'E	1966-68		
	Bugondo	1°37'N 32°57'E	1931-1960		
Uganda	Bukalasa	0°43'N 32°31'E	1963, 65-68	Kibale	0°34'N 30°21'E
	Kanywara	0°35'N 30°22'E	1969-72		
	Mbarara	0°37'S 30°39'E	1973		
	Kasese	0°11'N 30°06'E	1973		
Tanzania	Kigoma	4°53'S 29°38'E	1931-60, 1960-63, 68, 1971-73	Gombe	4°40'S 29°38'E

Table 4.6. Climatic data for weather stations listed in table 4.5.

Country (chimpanzee field site)	Weather station	Years of data	Mean Temp. (°C)	Max Temp. (°C)	Min Temp. (°C)	Rainfall (mm)	Rainy days
Uganda (Budongo)	Bugusege	1964	20.9	25.8	16.0	1743.6	174.0
	Arapai	1966-68	23.1	28.9	17.0	1978.6	121.0
	Bugondo	1931-1960	*	*	*	1279.0	104.0
		Mean	*22.0*	*27.4*	*16.5*	*1667.1*	*133.0*
Uganda (Kibale)	Bukalasa	1963, 65-72	22.5	28.3	16.7	1254.8	130.0
			22.8	29.0	16.8	1389.8	126.0
	Kanywara	1969-72	19.5	25.0	14.0	1446.9	142.0
	Mbarara	1973	19.1	30.2	7.8	1023.8	107.0
	Kasese	1973	24.1	30.6	17.5	776.2	94.0
		Mean	*21.6*	*28.6*	*14.6*	*1178.3*	*120.0*
Tanzania (Gombe)	Kigoma	1931-60,	*	*	*	953.0	94.0
		1960-63,	23.3	28.9	14.9	1092.2	116.0
		68,	23.3	27.7	18.9	1140.4	107.0
		1971-74	23.4	28.0	18.9	1021.9	94.0
		Mean	*23.3*	*28.2*	*17.6*	*1051.9*	*103.0*

5. Long-term and study year data: Chimpanzee publications

Table 4.7. provides a summary of all climate data from the literature, data available, and years of data.

Table 4.7. Summary of climate data from the chimpanzee literature.

Field site	Reference	Notes	Mean annual rainfall (mm)	Mean annual temperature (°C)
Pan troglodytes				
Mt. Assirik	Baldwin *et al.* (1981)		*	26.5
	McGrew *et al.* (1981)		885.0	
Budongo	Sugiyama (1968)	Middle of forest (1963 - 67)	1426.5	26-30
Bossou	No exact record (Sugiyama & Koman 1987)	April-Nov (90% of annual rainfall)	~3000.0	*
Gombe	McGrew *et al.* (1981)	5 year average Kakombe Valley (1968-70, 1973-74)	1495mm	23.5
		2 year average (1973-74)	1417mm	*
Kasakati	Izawa & Itani (1966)	1963-4	*	22.9
Kibale	Chapman *et al.* (1994)	1987-1991	1832.0	23.3
	Butynski (1990)	Kanywara (1977-84)	1570.0	23.3
	Isabiyre-Basuta (1988)		1475.0	
	Wrangham (1975)	Main camp (1972-73)	1309.5	*
Lopé	Tutin *et al.* (1991)	1984-1990	1536.0	*
	Doran (1992)	1984-1991	1498.0	25.6
	Wrogemann (1992)	1984-1989	1522.9	25.3
	White 1994	1984-1992	1506.0	25.5
Mahale (all)	McGrew *et al.* (1981)		1762.0	*
	Nishida *et al.* (1983)		2000.0	*
Mahale:Kansyana	Takasaki *et al.* (1990)	1973-1988	1817.8	*
	Collins & McGrew (1988)		1870.0	*
	Uehara (*pers. comm.*, cited in Moore 1992)		1399.9	*
	Uehara (1982)	1976	1788.9	*
	Uehara (1982)	1977	2007.5	*
	Uehara (1982)	1978	1903.5	*
Mahale:Myako	Takasaki *et al.* (1990)	1976-1984	1704.7	*
	Collins & McGrew (1988)		1653.0	*
	Uehara (*pers. comm.*, cited in Moore 1992)		1746.0	*
	Uehara (1982)	1976	1690.2	*
	Uehara (1982)	1977	1690.9	*
	Uehara (1982)	1978	1992.4	*
Mahale:Bilenge	Takasaki *et al.* (1990)		1327.9	*
	Collins & McGrew (1988)		1400.0	*
	Uehara (*pers. comm.*, cited in Moore 1992).		1933.0	*
	Uehara (1982)	1978	1332,7	*
Okorobiko	Jones & Sabater-Pi (1971)		3528.5	21.0

Table 4.7. (continued).

Field site	Reference	Notes	Mean annual rainfall (mm)	Mean annual temperature (°C)
Tai National Park	Boesch & Boesch (1989)		1800.0	24.0
Ugalla	Kortlandt (1983*b*)	Uvinza (10km from NW corner of chimpanzee range)	928.0	*
		Malagarasi (20km from NE corner, 20yr average)	892.0	*
		Mpanda (70km from south corner of range)	943.0	*
Pan paniscus				
Lomako Forest	Malenky (1990)	1980-1987	1903.1	*
Wamba	Kano (1984)		~2000.0	*
	Takayoshi *et al.* (1984)	1936-1959	2005.0	24.5

Where monthly data allowed, seasonality indices were calculated. Climatic data in the following categories was then available: mean annual rainfall (mm); Simpson's index of rainfall diversity (Z); DIV index of rainfall diversity; P>2t = number of months where rainfall is greater than twice the mean annual temperature; mean annual temperature (°C); Mo50 = number of months with <50mm rainfall; Mo100 = number of months with <100mm rainfall.

Table 4.8. summarises the sources of climate data from long- and short-term weather sources. Table 4.9. lists the data in full.

Notes:

All codes after the reference Hulme (1993) are tabulated in table 4.8. where the grid reference is given for the site. The code given, e.g. ZAIRE3 is the code given in my database of the Hulme (1993) data.

Mt. Assirik: The weather station Kolda (Nicholson *et al.* 1988) is quite some distant to the west of Mount Assirik, however on the same latitude, and is at a lower altitude than Mount Assirik. However, Tambacounda, Kédougou and Kolda are equidistant from Mount Assirik, forming a triangle. The mean of the three values is 1123mm, nearer to the value given by Kortlandt (1983a), corresponding to Kortlandt's (1983b) estimate of rainfall at Mount Assirk, 1100-1300mm.

Budongo: Eggeling's (1947) rainfall was recorded at the peripherary of the forest, therefore Kortlandt (1983a) multiplies the value by 1.25 to take this into account.

Kibale: The mean rainfall values from Nicholson *et al.* (1988) are much lower than those estimated for more recent years by Wrangham, Rogers & Isabyre-Basuta (1993) of 1570-1700mm (1987-1991). This is reflected in the means from Hulme (1993). The mean for 1987-1991 is 1469.9mm and for 1963-1972, 1448.74mm. Therefore the difference between the earlier data from Nicholson *et al.* (1988) and Wrangham *et al.* (1993) is not due to a significant difference in rainfall over time, but reflects more the fact that Bukulasa and Mbarara are not very close to the Kibale field site.

Gombe: The values given for weather stations close to Gombe range from 937-1819mm. The data in Nicholson *et al.* (1988) averages 959mm, almost identical to the 950mm estimated by Kortlandt (1983*a*). Kigoma is at a similar altitude to Gombe, and has a similar topography (Korltandt 1983*a*), making Kigoma a good surrogate weather station for Gombe.

Bossou: Beyla, the weather station cited in Nicholson *et al.* (1988) is not very proximate to Bossou.

Table 4.9. Summary of all climatic data available for the chimpanzee field sites

Chimp site	Weather source	Source site name	Years of data	Rain (mm)	DIV	Z	P>2t	Temp (°C)	Mo50	Mo100
Pan troglodytes										
Budongo	Eggeling (1947	Budongo	1933-43	1495.0	0.56	0.91	11	21.0	1	4
Budongo	Sugiyama (1968)	Budongo	1963	1565.5	0.76	1.00	10	21.0	2	5
Budongo	Nicholson *et al.* (1988)	Buttaba	1904-73	745.0	0.61	0.91	10	21.0	3	11
Budongo	Uganda dept. meteorology	Budongo	1931-40	1114.0	0.65	0.90	10	21.0	2	6
Budongo	Uganda dept. meteorology	Budongo	1941-50	1355.0	0.83	0.89	10	21.0	2	6
Budongo	Uganda dept. meteorology	Budongo	1951-60	1400.0	0.68	0.90	10	21.0	2	5
Budongo	Uganda dept. meteorology	Budongo	1931-60	1289.0	0.71	0.90	10	21.0	2	6
Budongo	Uganda dept. meteorology	Bugusege / Aarapai	1964, 66-68	1914.0	0.76	0.89	10	21.0	21	3
Mt. Assirik	McGrew *et al.* (1981)	Mt. Assirik	1976	891.0	1.18	0.84	6	29.0	6	8
Mt. Assirik	McGrew *et al.* (1981)	Mt. Assirik	1977	824.0	1.44	0.78	4	29.0	7	8
Mt. Assirik	McGrew *et al.* (1981)	Mt. Assirik	1978	1224.0	1.41	0.79	5	29.0	7	7
Mt. Assirik	McGrew *et al.* (1981)	Mt. Assirik	1979	879.0	1.33	0.81	6	29.0	6	8
Mt. Assirik	McGrew *et al.* (1981)	Mt. Assirik	1976-79	954.0	1.29	0.82	5	29.0	6	7
Mt. Assirik	Nicholson *et al.* (1988)	Kolda	1922-79	1194.0	1.45	0.78	5	29.0	7	7
Gombe	Tanzania dept. meteorology	Kigoma	1931-60	953.0	0.94	0.87	6	22.7	5	6
Gombe	Wrangham (1975)	Gombe	1973	1513.0	0.80	0.84	8	22.7	4	6
Gombe	Wrangham (1975)	Gombe	1974	1321.0	0.99	0.87	8	22.7	4	5
Gombe	Wrangham (1975)	Gombe	1973-4	1417.0	0.92	0.86	7	23.0	4	6
Gombe	Nicholson *et al.* (1988)	Kigoma	1922-82	959.0	0.92	0.89	8	23.0	4	6
Gombe	Tanzania dept. meteorology	Kigoma	1960-63, 1965-7	1086.9	0.92	0.89	8	23.0	5	6
Gombe	Hulme (1993)	TANZ2	1922-88	960.1	0.97	0.86	*	*	6	6
Kasakati	Hulme (1993)	TANZ2	1922-88	960.1	0.97	0.86	*	*	6	6
Kasakati	Nicholson *et al.* (1988)	Uvinza	1928-82	984.0	0.97	0.89	*	23.0	6	6
Mahale	McGrew *et al.* (1981)	Kansyana	1974	1693.0	1.13	0.83	8	23.0	5	5
Mahale	McGrew *et al.* (1981)	Kansyana	1975	1586.0	1.10	0.85	8	23.0	4	5
Mahale	McGrew *et al.* (1981)	Kansyana	1977	2008.0	1.10	0.84	8	23.0	4	4
Mahale	McGrew *et al.* (1981)	Kansyana	1974-77	1762.0	1.01	0.86	7	23.0	4	5
Mahale	Uehara (1982)	Myako	1976	1690.2	0.93	0.83	8	23.0	4	6
Mahale	Uehara (1982)	Myako	1977	1690.9	1.04	0.85	8	23.0	4	4
Mahale	Uehara (1982)	Myako	1978	1992.9	1.00	0.85	8	23.0	4	5
Mahale	Uehara (1982)	Kansyana	1976	1788.9	1.00	0.83	8	23.0	4	6
Mahale	Uehara (1982)	Kansyana	1977	2007.5	1.10	0.84	8	23.0	4	4
Mahale	Uehara (1982)	Kansyana	1978	1903.5	1.00	0.86	7	23.0	4	5
Mahale	Uehara (1982)	Bilenge	1978	1332.7	1.00	0.86	8	23.0	5	7
Mahale	Takasaki *et al.* (1990)	Myako	1976-84	1704.8	0.92	0.87	8	23.0	4	5
Mahale	Takasaki *et al.* (1990)	Kansyana	1973-88	1867.3	0.96	0.86	12	24.3	4	5
Bossou	Nicholson *et al.* (1988)	Beyla	1921-62	1779.0	0.81	0.89	**	**	3	4
Tai Forest	Nicholson *et al.* (1988)	Soubre	1940-79	1534.0	0.67	0.90	10	24.0	1	3
Kibale	Nicholson *et al.* (1988)	Mbarara	1912-83	923.0	0.59	0.92	**	**	3	8
Kibale	Uganda dept. meteorology	Kanywara/Bukulasa	1963, 65-72	1383.7	0.57	0.92	12	19.8	0	5
Pan paniscus										
Wamba	Hulme (1993)	ZAIRE3	1912-73	1709.8	0.44	0.91	**	**	0	2
Wamba	Nicholson *et al.* (1988)	Befori	1937-59	2211.0	0.41	0.92	12	23.6	0	0
Lomako	Malenky (1990)	Lomako	1980-84	1903.1	0.45	0.91	12	24.3	0	1
Lomako	Griffiths (1972)	Bafale	30 yrs*	2054.8	0.39	0.91	12	24.3	0	0
Lomako	Griffiths (1972)	Yangambe	30 yrs*	1810.6	0.43	0.92	**	**	0	2
Lomako	Hulme (1993)	ZAIRE3	1912-73	1709.8	0.44	0.91	**	**	0	2
LacTumba	Nicholson *et al.* (1988)	Mondombe	1932-59	2015.0	0.37	0.93	**	**	0	0
Yalosidi	Hulme (1993)	ZAIRE3	1912-73	1709.8	0.44	0.91	**	**	0	2
Yalosidi	Nicholson *et al.* (1988)	Tshibanda	1927-49	1869.0	0.59	0.91	**	**	1	3

* unspecified period; ** no temperature data (therefore cannot compute P>2t).

Rain = mean annual rainfall (mm); ***Z*** = Simpson's index of rainfall diversity; ***DIV*** = index of rainfall diversity; ***P>2t*** = number of months where rainfall is greater than twice the mean annual temperature; mean annual temperature (°C); ***Mo50*** = number of months with <50mm rainfall; ***Mo100*** = number of months with <100mm rainfall.

4.2.3. Seasonality at chimpanzee field sites

The study of chimpanzees in hot, dry habitats has been thought to be important in modelling the behavioural ecology of early hominids in a referential framework (see section 1.1.2.i) (Kortlandt 1983*b*, 1984; Laporte & Zihlman 1983). Chimpanzees' adaptations to arid conditions may provide insights into the adaptations of early hominids in similar habitats (e.g. Suzuki 1969). A comparison of chimpanzees in a range of habitat types, may also shed light on the sources and functions of the variability in chimpanzee behavioural ecology and social structure (McGrew 1983; McGrew *et al.* 1981).

Mount Assirik, Kasakati, Filabanga and Ugalla may be classified as savanna habitats (Moore 1992). The definition of a savanna is broad, but most definitions focus on the domination of C_4 fixing grasses. Savanna ecosystems range from treeless plains to closed woodland habitats (Huntley 1982). Tropical savannas are further defined as seasonal ecosystems with a continuous herbaceous component, and a discontinuous woody component (Frost *et al.* 1986). A more detailed understanding of the relationship between the partitioning of water between shrub and grasslands in savannas is needed if we are to predict changes in plant community structure with changing precipitation (le Roux *et al* 1995).

Moore (1992) tabulated rainfall at chimpanzee study sites, incorporating data from a combination of sources (see table 4.10). Moore (1992) attempted to define seasonality in three ways. Firstly by Q, which is defined by;

Q = (number of dry months / wet months) × 100)

(where a dry month has ≤60mm rainfall, and a wet month has >100mm rainfall (Whitmore 1975)).

The second measure of seasonality was simply the number of dry months. Figure 4.4 illustrates the relationship between Q and mean annual rainfall for chimpanzee (not bonobo) field sites. Assirk and Ugalla have the highest value of Q, and hence greater seasonality of rainfall. The rainfall estimates for Gombe in table 4.10 appear too high compared to those listed in table 4.9.

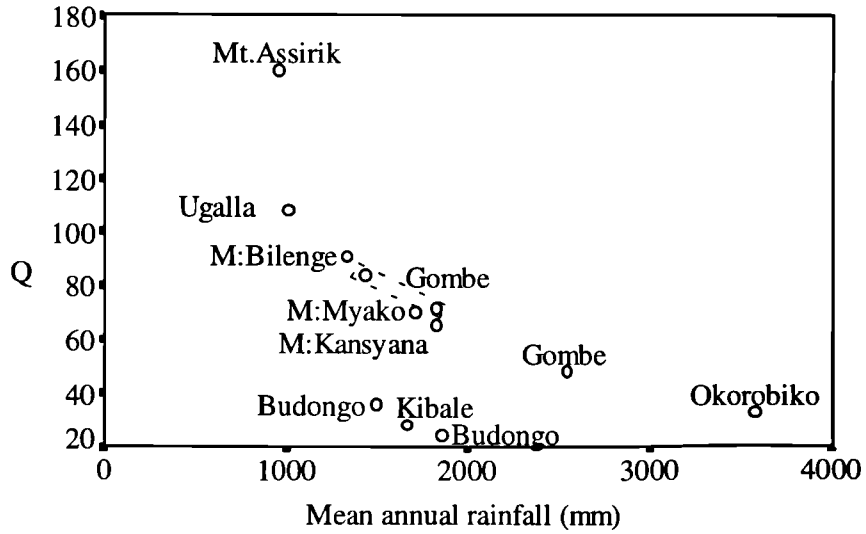
Table 4.10. Rainfall and rainfall seasonality at Chimpanzee study sites

Site	Rainfall (mm) (Mean ± SE)	No. of months ≤60mm rain	Mean ± of *Q*'s	*Q* of mean	Period (*N*)
Mt. Okorobiko	2112.0	3.0	*	43.0	** (13)
	3538.5	3.0	33.3	*	1967 (1)
Budongo	1489.3 ± 196.6	2.6 ± 0.9	36.3 ± 16.4	13.0	1934-42 (9)
	1861.7 ± 245.6	2.0 ± 0.9	25.3 ± 11.8	11.0	
Kibale	1536.0	1.0	*	14.0	1941-70 (30)
	1664.0	2.0	28.6	*	1977 (1)
Gombe	1819.8 ± 580.7	4.3 ± 0.9	71.8 ± 33.4	50.0	1968-87 (20)
	2542.7 ± 169.6	3.7 ± 0.8	48.6 ± 11.3	50.0	1976-82 (7)
	1430.6 ± 225.1	4.6 ± 0.9	84.3 ± 33.4	67.0	remainder (13)
Mahale:					
Kansyana	1817.8 ± 184.4	4.4 ± 0.8	66.0 ± 14.9	57.0	1974-88 (14)
Myako	1704.8 ± 189.2	4.7 ± 0.7	70.4 ± 17.8	57.0	1976-84 (9)
Bilenge	1327.9 ± 139.1	5.0 ± 0.0	91.5 ± 9.8	83.0	1978-80; 1982(4)
Ugalla	1012.3 ± 139.1	5.2 ± 0.8	108.8 ± 38.7	83.0	1973-88 (16)
Kasakati	962.0	6.0	*	100.0	1941-70 (30)
Mt. Assirik	954.5 ± 182.0	6.8 ± 1.0	160.0 ± 27.1	140.0	1976-79 (4)

* = not calculated due to insufficient data (n = 1, or only averages presented in the data source); ** unknown period. *Q* = (dry months / wet months) × 100. Where a dry month has ≤60mm rainfall, and a wet month >100mm rainfall.

Sources: ***Mt. Okorobiko***: top line, unspecified period at Neifang (Griffiths 1972), lower line from Jones & Sabater-Pi (1971). ***Budongo***: Data from Eggeling (1947), lower line corrected (× 1.25) for an estimated greater rainfall in the forest). ***Kibale***: Data from Ft. Portal (~16km NW of forest), top line Anon (1983), bottom line Ghiglieri (1984). ***Gombe***: Anon (1988). ***Mahale***: Anon (1988), Takasaki *et al.* 1990). ***Ugalla***: Data from Uvinza (~10km NW of nearest observations of chimpanzees) (Anon 1988). ***Kasakati***: Data from Kigoma (Anon 1984), ~70km NW. ***Mt. Assirik***: Data from McGrew *et al.* (1981).

Figure 4.4. Rainfall seasonality (Q) against mean annual rainfall for chimpanzee field sites. Data from Moore (1992). See table 4.10. for data sources.



Q = (dry months / wet months) × 100, Where a dry month has ≤60mm rainfall, and a wet month >100mm rainfall. **M:** = Mahale.

Kortlandt (1983*b*) in reply to the climate data presented in McGrew *et al.* (1981) commented on the high values cited for Gombe. McGrew *et al.* (1981) cited two rainfall values for Gombe:

(1) (McGrew *et al.* 1981; table 2), 5 year average Kakombe Valley (1968-70; 1973-74) **1495mm.**

(2) (McGrew *et al.* 1981; table 3), 2 year average, Gombe (1973-74) **1417mm.**

Kortlandt (1983*b*) acquired climate records from the nearby site of Kasakati (1km north of Kasakombe), for the years 1969-74, for which the mean annual rainfall was **1437mm.** Compared to Kigoma (41km to the North), the mean annual rainfall for Kasakombe was relatively high. Gombe's location on a map of rainfall isohyets (Bultot 1971), Gombe falls between 1000-1100mm (Kortlandt 1983*b*). The statistical chance of rainfall greater than 1400mm was one in 40 years.

If seasonality is plotted against rainfall from the Nicholson *et al.* (1988) database, and from data in table 4.10. a different pattern emerges with respect to the driest chimpanzee field site. Furthermore, the Moore (1992) data did not include bonobos. Figure 4.5 plots seasonality against rainfall from the Nicholson *et al.* (1988) database (see table 4.3). Seasonality is indexed by Simpson's index of rainfall diversity for illustration, although there are numerous other seasonality indices (see chapter 2). The Nicholson *et al.* (1988) database assigns the lowest mean annual rainfall to Budongo, not to Mount Assirik. This is not due to an inaccuracy in the geographic location of the weather station for Budongo (Butaba) which is close to the map reference for Budongo. All map references are accurately placed, with the exception of the Taï Forest weather station (Soubré). Figures 4.4 to 4.6 all clearly show Mount Assirik to be the most seasonal habitat, although not necessarily the driest. Figure 4.6 gives Ugalla and Gombe lower mean annual rainfall than Mount Assirik, followed by Budongo. The lower values selected for Gombe and Ugalla, follow the suggestions of Kortlandt (1983; see above). In both figures 4.1.a & b; 4.6 and 4.7, the bonobo field sites have both the highest rainfall, and least seasonality in the distribution of rainfall (more evenly distributed throughout the year). The greater seasonality in rainfall in savanna habitats (Bourliére &

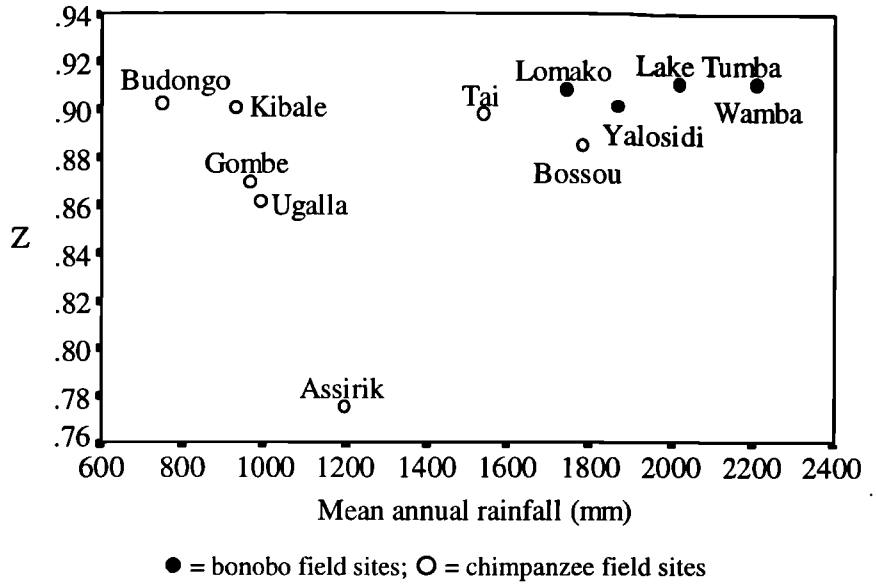
Hadley 1983) is likely to result in seasonality in the availability of resources. Relative to woodlands, savanna woodlands are drier and rainfall is more seasonal (McGrew *et al.* 1981; Moore 1992). Water may be seasonally hard to locate in these habitats, and consequently thermoregulation becomes more demanding.

Conclusion

The previous section (4.2) summarised available meteorological data for the main chimpanzee field sites for which there are long-term behavioural data. These data will be used in subsequent models of chimpanzee socioecology, therefore a detailed consideration of the sources of climate data was necessary. Long-term climate records located close to chimpanzee field sites were collated from a combination of government publications, world weather compilations and study site records. Different climate data was available from each source, notably the lack of temperature data from some long-term compilations. Nevertheless, temperature does not vary significantly across the chimpanzee field sites, and short-term field site data were considered sufficient. The analyses in chapter 2 revealed that the proximity of the climate data to a study site, was more important than having inaccurately located long-term climate data. The proximity of climate data in combination with duration of the record were shown to be particularly important when comparing seasonality among the chimpanzee sites. Therefore, the climate data used in the analyses presented in this chapter will be drawn from table 4.9, from those sources close to the chimpanzee field sites.

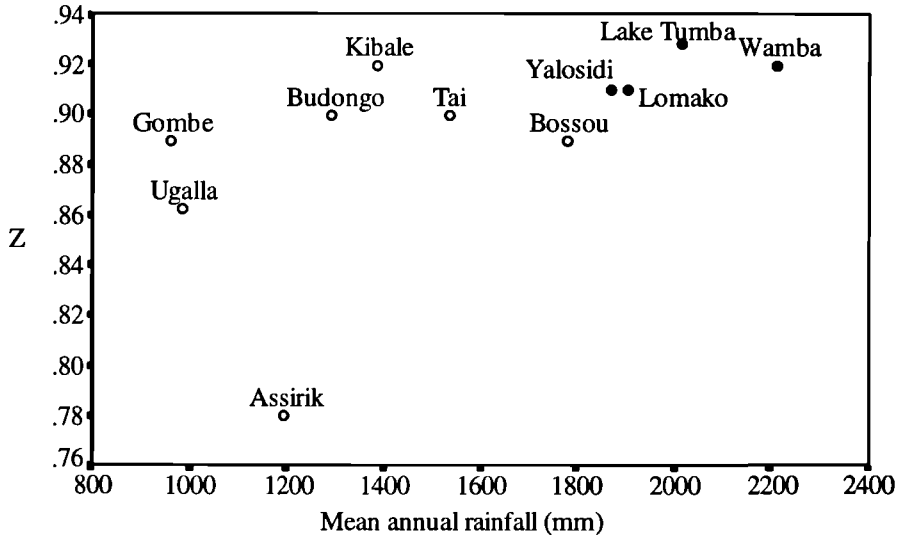
In subsequent sections where functional equations are developed, relating behavioural to environmental variables, long-term climate data (see table 4.9) will be used where possible. In the following section I review the behavioural data that will be related to the climatic variables collated in this section.

Figure 4.6. Simpson's index of rainfall diversity against mean annual rainfall for chimpanzee and bonobo field sites. Data from Nicholson *et al.* (1988), see table 4.3 for data.



● = bonobo field sites; O = chimpanzee field sites

Figure 4.7. Simpson's index of rainfall diversity against mean annual rainfall for chimpanzee and bonobo field sites. Data from combination of sources, emphasising long-term and proximity to field site (see table 4.9 for data).



● = bonobo field sites; O = chimpanzee field sites

Sources (see table 4.9. for data). For each field site; reference (date), weather station (years of data): ***Assirik***: Nicholson *et al.* (1988), Kolda (1922-79); ***Bossou***: Nicholson *et al.* (1988), Beyla (1921-62); ***Budongo***: Uganda dept. Meteorology, Bugusege/Aarapai (1964, 66-68); ***Gombe***: Tanzania dep. Meteorology, Kigoma (1960, 63, 65-67); ***Kibale***: Uganda dept. Meteorology, Kanywara/Bukulasa (1963, 65, 67); ***Lomako***: Malenky (1990), Lomako (1980-84); ***Lake Tumba***: Nicholson *et al.* (1988), Mondombe (1932-59); ***Ugalla***: Nicholson *et al.* (1988), Uvinza (1928-82); ***Wamba***: Nicholson *et al.* (1988), Befori (1937-59); ***Yalosidi***: Nicholson *et al.* (1988), Tshibinda (1927-49).

4.3. BEHAVIOURAL DATA

4.3.1. Introduction

Chimpanzees and bonobos were considered together in this analysis, for similar reasons that all *Papio* baboon species were analysed together in chapter 3. Species in the systems models presented in this thesis, are viewed as ecological species. Ecological species are defined as those species that happen to share a set of ecologically relevant characteristics (e.g. body size) and a particular bauplan with respect to dietary and reproductive specialisations. This means that we can consider the difference between species as being mainly due to differences in either body size or environmental conditions.

Molecular evidence lends further support to the consideration of chimpanzees and bonobos together in the model. Chimpanzees and bonobos diverged about 2-3mya (Cronin 1983; Goodman *et al.*, 1994). On the basis of MtDNA divergence, Morin *et al.* (1994) have concluded that *Pan troglodytes verus* and the other two chimpanzee subspecies (*Pan troglodytes troglodytes* and *Pan troglodytes schweinfurtii*) diverged about 1.6mya, roughly contemporaneously with the origin of *Homo erectus* (Moore 1996). In addition *P. t. verus* cannot be distinguished reliably from *Pan troglodytes troglodytes* or *Pan troglodytes schweinfurtii* on morphological grounds (Shea *et al.* 1993). However, there are some distinctions in overall body proportions between bonobos and chimpanzees (Morbeck & Zihlman 1989). Genetic compatibility and similarity in origin may be inferred from the fact that bonobo and chimpanzee hybridisation has been recorded in captivity (Vervaecke & van Elsacker 1992). Mountain and lowland gorillas differ in mitochondrial COII sequences more than do chimpanzees and bonobos (Ruvulo *et al.* 1994), suggesting a divergence date of almost 3mya (Morell 1994); again morphological differences are slight. Lowland gorillas and chimpanzees have a molecular divergence date about 5.5-7mya (Hasegawa 1992; see discussion in Goodman *et al.*, 1994; Zihlman 1996). Chimpanzees and gorillas are similar in shape and diet, and gorillas are viewed by some as essentially allometrically scaled-up versions of chimpanzees (Shea 1990; Doran 1996). All of these comparisons

indirectly suggest much morphological conservatism in the African pongid lineage, and therefore support the notion that the last common ancestor (LCA) would have resembled a chimpanzee.

Overlapping habitats and climate provide further support for combining chimpanzees and bonobos in this analysis. Chimpanzees and bonobos are allopatric, separated by the Zaire River. The latitudinal and longitudinal distribution of bonobos is entirely overlapped by that of chimpanzees (bonobo latitudes: 2°N to 4°S; chimpanzee latitudes: 13°N to 7°S). Consequently, the range of climates experienced by bonobos is a sub-set of those experienced by chimpanzees.

Chimpanzees and bonobos are also considered together in this analysis because of their broad similarity in ecological adaptation. Nevertheless, there are differences in behavioural ecology and social organisation between chimpanzees and bonobos, which have been the focus of recent field studies. Both bonobos and chimpanzees share a fission fusion social system, in which individuals within a community associate in small parties of variable size and composition. Party compositions change less frequently among bonobos, than chimpanzees at Taï (Boesch 1991), and at Gombe (Halperin 1979), but not more than the chimpanzees at Bossou (Sugiyama 1984). Unlike chimpanzees, lone bonobo individuals are rarely observed, and are usually males (White 1988). The pattern of fission and fusion is very similar among chimpanzees and bonobos (Chapman *et al.* 1994). However, during feeding at abundant food sources, chimpanzees have a tendency to disperse (e.g. Ghiglieri 1984) while bonobos coalesce (White 1986). Similarly during feeding, chimpanzee males tend to coalesce, whilst male bonobos disperse (White & Chapman 1994). Bonobos tend to form larger sleeping parties than chimpanzees (Furuichi 1989; Fruth & Hohmann 1994). Female members of chimpanzee parties tend to contain females within their separate, yet overlapping core areas. However, oestrous bonobo females have a different distribution, potentially having core areas larger than males (White & Lanjouw 1992). One of the most obvious unique behaviours of bonobos is genito-genito (G-G) rubbing between females. G-G rubbing is suggested to have a number of functions: association with feeding (Kano 1980; Kuroda

1980; Thompson-Handler *et al.* 1984), reducing feeding competition (White & Lanjouw 1992) and co-operation among females for patch defence (White 1986; White & Lanjouw 1992).

The differences in socioecology between chimpanzees and bonobos have been hypothesised to be due to reduced feeding competition in bonobos, which permits larger party sizes (White 1986; White & Wrangham 1988). However, more recent studies have shown that the rainforest chimpanzees at Kibale used patch sizes comparable to the bonobos at Lomako (Chapman *et al.* 1994). Additionally, the Kibale chimpanzees have similar female-female affiliation to other populations of *Pan troglodytes.* Seasonal variation in food distribution was greater for *P. troglodytes* at Kibale, than *P. paniscus* at Lomako, evidenced by a correlation between mean monthly party size and food abundance (Wrangham *et al.* 1992; see also Taï Forest: Doran 1989). Therefore relative, rather than absolute food abundance may be the selective force driving the difference in social organisation between the two species (Malenky 1990). However, fruiting seasonality in lowland forests is strongly related to latitude (van Schaik *et al.* 1993), therefore fruiting seasonality is unlikely to be significantly different between chimpanzees and bonobos. There is currently no evidence for consistent differences in plant structure and dynamics between forests occupied by chimpanzees or bonobos (van Schaik *et al.* 1993). One further hypothesis regarding the difference in feeding competition of chimpanzees and bonobos, is the availability of terrestrial herbaceous vegetation (THV). Gorillas only live north of the Zaire River, sympatric with most of the range of chimpanzees, but never with the bonobos. The gorilla diet is restricted to THV, resulting in low within-group feeding competition (Watts 1994; Janson & Goldsmith 1995). It is therefore hypothesised that gorilla consumption of THV reduces that available to sympatric chimpanzees (Wrangham 1986). Bonobos have more THV available, potentially explaining the greater stability in bonobo group structure. Only one study has directly compared the THV consumption of bonobos and chimpanzees (Malenky & Wrangham 1994), finding significantly greater THV consumption among bonobos. THV has also been hypothesised as a fall back food, exploited when fruit becomes scarce

(Wamba: Kano & Mulavwa 1984; Ndoko: Kuroda *et al.* 1996; Lopé: Tutin *et al.* 1991; Kibale: Wrangham *et al.* 1991; Kahuzi-Biega: Yamagiwa *et al.* 1996).

Less is known about feeding competition for the west African 'savanna' chimpanzees (Moore 1992). Relative to the forest chimpanzees, there are fewer sympatric species competing for food in the savanna chimpanzees. Elephants (*Loxodontata africana*), browsing antelope (e.g. *Tragelaphus scriptus*), vervet monkeys (*Cercopithecus aethiops*) and especially baboons (*Papio* spp.) overlap in diet with chimpanzees (Peters & O'Brien 1981; but see McGrew *et al.* 1982; Collins & McGrew 1988). The differences between savanna woodland and more forested chimpanzee habitats may promote behavioural differentiation between savanna and forest chimpanzees.

Despite these differences, emphasis must be placed upon the fact that species do *not* show species-typical behaviour. Furthermore, among bonobos, differences in behavioural strategies between sites cannot always be related to inter-site ecological differences.

4.3.2. Time budget data

It has previously been noted (Jolly 1972; Marsh 1981) that the method of collection of time budgets was critical in comparative analyses. Marsh (1981) tried to compare his study of red colobus (*Colobus badius rufomitratus*) with previous studies at the same study site and found significant differences. Time budgets can be scored in several ways. For example, instantaneous (recording time budgets the moment the animal was detected), or measured during sustained activities). The method of scoring time budgets is thought to make a difference to the time budgets recorded. However, in the comparison of two time budget studies of red colobus (Marsh 1981), methodological problems were not the only source of differences between studies. For example, differences in feeding time between sites may have been compensated for by changes in rates of food intake (Marsh 1981). Because of the potential bias in the method of time

budget collection, I have outlined below the methods of collection of the time budgets of the chimpanzee data in tables 4.11. and 4.12.

There are three problems inherent in time-budget data (Rugg & Buech 1990). Firstly, that behaviour during unknown periods may differ from that of known periods (i.e. that data are not missed at random) (see Altmann 1974). Secondly, that the activity period can be unevenly sampled, either directly, or as a result of unknown periods. This could create potential bias when the data are pooled, rather than weighted by their contribution to the time budget. Thirdly, a pick-up bias may be important, that an observer will locate an animal for observation depending on the animals' activity state (Altmann *op. cit.*). As a result of these potential biases, statistical tests on time-budget data are viewed by Rugg & Buech (1990) as unsatisfactory, and they developed techniques based on stochastic models to analyse time-budgets.

i. Methods of time budget collection

Mahale (Chimpanzees)

Time budgets are calculated as a percentage of the total observation time spent in activities by 9 focal animals (1 old adult male, 1 prime adult male, 2 old adult females, 2 prime adult females, 2 lactating young adult females and 1 pregnant female). There was no significant difference in the time spent in each activity category in relation to age or sex. A total of 361.69 hours of focal animal observations were used in the analysis of activity patterns. The study was conducted on the M-group, which at the time of study consisted of 100 individuals. Focal animals were followed for as long as possible, and data recorded in four categories;

1. *Foraging*: Feeding in a fixed location, or moving between feeding spots in a tree or on the ground, where movement without feeding was less than 60 seconds.
2. *Resting*: Sitting or laying down quietly, and/or engaging in brief social interactions (e.g. appeasement, aggression etc.).
3. *Grooming*: Grooming activity usually occurs during rest periods but here it is calculated separately.

4. *Travelling*: Walking, taking short (<60 second) rests, including movement between locations of other activities, such as foraging, resting or grooming.

Table 4.11. Data available on activity budgets of chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*).

Site	Sex	% Feed	% Travel	% Rest	% Groom*	%Other	Reference
Pan troglodytes							
Mahale[a]	M/F	29.7	19.6	38.6	*	*	Huffman, 1990
Okorobiko[b]	M/F	40.8	27.5	31.7	*	*	Sabater-Pi, 1979
Gombe[c]	M	55.7	13.8	30.3	*	*	Wrangham, 1975
Kibale[d]	M	67	15	32	*	*	Ghiglieri, 1984
	F	57	15	34	*	*	"
	M/F	62	15	33	*	*	"
Pan paniscus							
Wamba[e]	M/F	18.0	13.0	43.0	*	13.0(20.0)‡	Kano & Mulavwa, 1984
Lomako[f]	M/F	40.4	16.1	31.9	6.3 (5.7)**	*	White, 1992*b*

* No available data / not an activity category used in that particular study.

Notes on methods of study:

a) ***Mahale:*** Distribution of time as a percentage of total observation time by focal individuals (n = 9. Males: 1 old adult; 1 prime adult. Females: 2 old adults; 2 prime adults; 3 young adults (2 with independent young, 1 nullipar). Values in the table above are means for all age/sex classes, since there were no significant differences between them.

b) ***Okorobiko:*** Values (figure 8, p.275) in Sabater-Pi (1979). Values given above are means from hourly time budgets (6 a.m. - 6 p.m.). The values are means from two study periods; July 13, 1966 to February 19, 1969; June 1963 to September 1964.

c) ***Gombe:*** Percent of 30 min points spent in different activities (n = 54 all-day-observations). Focal observations on males only.

d) ***Kibale:*** Data read off bar chart (Figure 6, Ghiglieri, 1984). Diurnal activity patterns of male and female chimpanzees beyond infant age. Data are summations of 5-min observations during each hour. Sample period December 1976 to May 1978. Sampled between 6:00h and 20:00h. Data given in this table are means for males and females, which are not significantly different. Females: feed 57%; travel 15%; rest 34. Males: feed 66%; travel 15%; rest 32%. The activity budget does not total 100% due to slight inaccuracies in measuring from the original figure. Because data is read off from a graph, percentages. due to rounding, may sum to more than 100%.

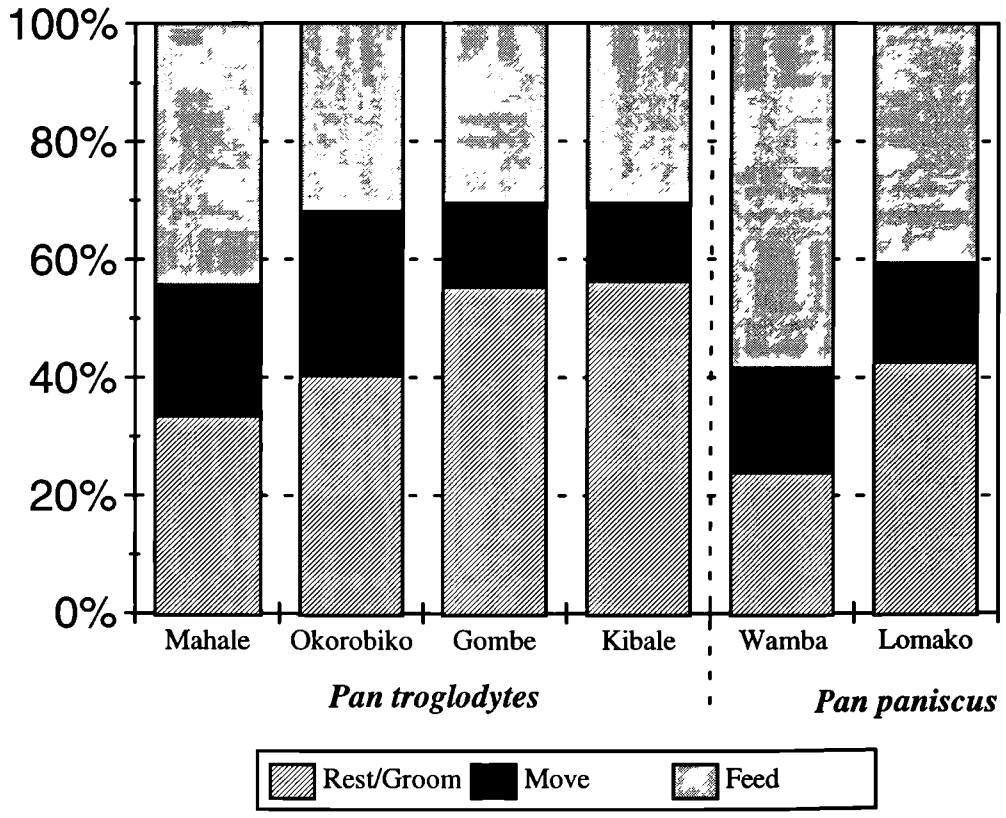
e) ***Wamba:*** Diurnal activities were divided into five categories:
Arboreal feeding: party members feeding in trees
Arboreal resting: Inactivity in trees, includes allo- or self-grooming and social or individual play, and making of day nest.
Travelling: After 10m arboreal travelling, the rest is usually terrestrial.
Terrestrial activities: includes all activities on the ground other than travelling.
Other.
To match the categories given in other studies; Arboreal feeding = feed; arboreal rest = rest; travel = travel; terrestrial activities (+other ‡) = other.

f) ***Lomako:*** n = 7754 time points.
* Grooming and other 'social' activities are included in the resting category except for Lomako.
** 6.3% total 'inter-activity', of which 5.7% is spent grooming.

Table 4.12. Data available on Activity budgets of Chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*). Time budget categories modified in Lomako to fit other studies. 'Other' category omitted from Wamba data.

Site	Sex	% Feed	% Travel	% Rest / groom	Reference
Pan troglodytes					
Mahale[a]	M/F	29.7	19.6	38.6	Huffman, 1990
Okorobiko[b]	M/F	40.8	27.5	31.7	Sabater-Pi, 1979
Gombe[c]	M	55.7	13.8	30.3	Wrangham, 1975
Kibale[d]	M	67	15	32	Ghiglieri, 1984
	F	57	15	34	"
	M/F	62	15	33	"
Pan paniscus					
Wamba[e]	M/F	18.0	13.0	43.0	Kano & Mulavwa, 1984
Lomako[f]	M/F	40.4	16.1	38.2	White, 1992*b*

Figure 4.8. 100% histogram of chimpanzee time budgets (see table 4.12. for data).



Kibale (Chimpanzees)

The activity budgets are of male and females beyond infancy. The data are thought to be biased since approximately half of all observations were made during fruit tree vigils (Ghiglieri 1984), which tends to under-sample travelling time. However, when considering non-vigil time, travelling time was over-sampled to a greater degree. The difference in time budgets between males and females at Kibale is notable. Males spent more time moving and more time feeding than females. Adult male chimpanzees are only 1.3 times as heavy as females, a level of sexual dimorphism and associated metabolic demands that would seem to be insufficient to explain the differences in time budgets. Increased travel may result from non-foraging concerns. For example, patrolling the community home range and increasing opportunities to locate and mate with oestrous females.

Wamba (Bonobos)

The data come from studies conducted on the E-group at Wamba. The primary behavioural sampling method was random sampling. Diurnal activities of parties at Wamba from the time of awakening and leaving the sleeping nest (5:00 to 6:00) to the time of making and settling into a new nest (17:00 - 19:00) were classified into five categories.

1. *Arboreal feeding*: Includes activities when feeding in trees.
2. *Arboreal resting*: Where most party members were inactive in trees, or allo-grooming, social or individual play. All resting places were at or near food sources.
3. *Travelling*: Usually occurs during resting time. In general the ground is used for travelling after the first several tens of meters of arboreal travel.
4. *Terrestrial activities*: All activities on the ground, other than travelling. The time budgets are presented as hourly activity budgets.

Lomako (Bonobos)

No detail was given in the published source (White 1992) as to the criteria for recording time budget categories.

4.3.3. Compilation of databases

Besides time budget data, data were collated on as many demographic and environmental variables as possible. Data were only used where there was sufficient *comparable* data between chimpanzee and bonobo field studies. Two behavioural databases will be considered in this chapter. The first tabulates data from 19 chimpanzee and bonobo field sites (table 4.13), providing data on the core behavioural variables (time budgets, group size, day journey length, density and home range size) and environmental variables (temperature, rainfall seasonality and rainfall). As shown in tables 4.11 and 4.12, time budget data were only available for 6 field sites (Gombe, Mahale, Okorobiko, Kibale, Lomako and Wamba). The second database tabulates data only on those six field sites with time budget data. A wider variety of behavioural and environmental data are provided (table 4.14).

In the following section I shall use these data to develop functional multiple regression equations, relating behavioural and environmental variables. These equations will be used as inputs in a model of chimpanzee maximum ecologically tolerable group size (for methods see section 3.2).

4.4. SYSTEMS MODEL OF CHIMPANZEE SOCIOECOLOGY

4.4.1. Introduction

The aim of this chapter is to further develop the systems models of primate socioecology developed on baboons and gelada baboons (see section 3.3). After having carefully defined the behavioural and environmental data, the next step is to develop functional step-wise regression equations. The same statistical techniques outline in section 3.4.3. will be used here. In the following section I shall outline the results obtained from stepwise regression equations set through the behavioural and environmental data above.

Table 4.13. Summary of all behavioural data for chimpanzees and bonobos collated from the literature (see table 4.12 for time budget data).

SITE	PERIOD	PARSIZ	DENSITY	HOMRNG	WTM	WTF	WTRATIO	TMAX	ABMAX	TMIN	ABMIN
Budongo	Sugiyama 1968	4.40	6.70	7.50	*	*	*	28.00	35.00	14.00	10.00
Budongo	Reynolds & Reynolds 1965	3.90	3.40	20.00	*	*	*	28.00	35.00	14.00	10.00
Budongo	Suzuki 1971	*	6.00	14.00	*	*	*	28.00	35.00	14.00	10.00
Gombe	Before fission 1965-71	*	*	*	*	*	*	*	*	*	*
Gombe	Goodall 1968, 1986	4.00	1.40	38.00	39.50	29.80	75.40	*	*	*	*
Gombe	Wrangham 1975	*	2.50	12.00	*	*	*	*	*	*	*
Mahale	Nishida 1968	6.20	*	*	42.50	35.20	83.80	27.00	36.00	19.00	16.00
Mahale	Nishida & Tachibana 1987 (71-72)	*	*	*	*	*	*	27.00	36.00	19.00	16.00
Mahale	K-group	10.40	5.70	*	*	*	*	27.00	36.00	19.00	16.00
Mahale	M-group	13.40	5.70	*	*	*	*	27.00	36.00	19.00	16.00
Bossou	Sugiyama & Koman 1979	5.50	3.50	*	*	*	*	*	*	*	*
Bossou	Sugiyama 1968	*	*	*	*	*	*	*	*	*	*
Bossou	Sugiyama 1981	6.00	*	*	*	*	*	*	*	*	*
Bossou	Sugiyama 1994	*	*	*	*	*	*	*	*	*	*
Okorobiko	Sabater Pi 1979	9.90	*	*	*	*	*	24.00	33.00	18.00	15.00
Assirik	Tutin *et al.* 1983	4.00	0.09	306.00	*	*	*	35.00	44.00	23.00	16.00
Tai	Boesch 1991	8.40	*	*	*	*	*	*	*	*	*
Kibale	Ghiglieri 1984, 1986	2.60	2.20	*	*	*	*	*	*	*	*
Kibale	White & Wrangham 1988	*	2.20	*	*	*	*	*	*	*	*
Kibale	Wrangham *et al.* 1996	5.24	2.20	*	*	*	*	*	*	*	*
Wamba	Kuruda 1979 (B-group)	16.90	3.00	45.00	*	*	*	*	*	*	*
Wamba	Kano 1980 (K-group)	*	1.70	*	*	*	*	*	*	*	*
Yalosidi	Kano 1983	8.60	2.00	*	*	*	*	*	*	*	*
Yalosidi	Uehara 1988	*	*	*	*	*	*	*	*	*	*
Yalosidi	Kuruda 1979	16.90	*	*	*	*	*	*	*	*	*
Lomako	Kano 1983	8.50	*	*	*	*	*	*	*	*	*
Lomako	Badrian & Badrian 1984	7.90	2.00	*	*	*	*	*	*	*	*
Lomako	White & Wrangham 1988	*	*	*	*	*	*	*	*	*	*
Lomako	Malenky & Stiles 1991	5.40	*	*	*	*	*	*	*	*	*
Lomako	Wrangham *et al.* 1996	5.40	*	*	*	*	*	*	*	*	*
Kasakati	Suzuki 1969	*	0.63	*	*	*	*	28.00	34.00	19.00	8.00
Kasakati	Izawa 1970	*	0.35	123.00	*	*	*	28.00	34.00	19.00	8.00
Filabanga	Kano 1971	*	0.20	*	*	*	*	*	*	*	*
Ugalla	Kano 1972	*	0.10	255.00	*	*	*	*	*	*	*

*** = missing values; Key: PARSIZ = party size; DEN = density (animals /km^2); HOMRNGE = home range (km^2); WTM = mean male body weight (kg); WTF = mean female body weight (kg); WTRATIO = ratio of male: female body weight; TMAX = mean maximum temperature (°C); TMIN = mean minimum temperature (°C); TABMIN = mean absolute minimum temperature (°C).**

Table 4.14. Behavioural and environmental data from field sites with time budget data (n = 6).

Site	% Feed	% Move	% Rest	FRU	LEAF	STEM	SEED	ANIM
Mahale	29.70	19.60	38.50	60.80	10.80	6.30	12.00	10.40
Okorobiko	40.80	27.50	31.70	44.83	31.75	*	7.66	3.83
Kibale	62.00	15.00	33.00	82.10	8.00	11.70	*	0.20
Gombe	55.70	13.80	30.30	*	*	*	*	*
Wamba	18.00	13.00	43.00	83.40	15.20	*	*	1.20
Lomako	40.40	16.10	38.20	49.00	21.00	15.00	9.00	*

Site	Fwt	Mwt	mixed	mum	bisex	unisex	lone	m adult
Mahale	32.50	40.75	*	*	*	*	*	10.68
Okorobiko	32.50	40.75	*	*	*	*	*	*
Kibale	32.50	40.75	40.30	22.80	10.40	16.70	4.80	31.81
Gombe	32.50	40.75	30.00	24.00	18.00	10.00	18.00	*
Wamba	32.50	40.75	74.20	4.90	2.50	2.50	6.10	22.05
Lomako	32.50	40.75	88.40	5.20	7.90	4.70	18.90	*

Site	m sadult	m juv	m inf	f adult	f sadult	f juv	f inf	mtot
Mahale	8.74	2.91	8.74	37.86	9.71	9.71	11.65	31.07
Okorobiko	*	*	*	*	*	*	*	*
Kibale	4.55	9.09	9.09	27.30	9.09	9.09	4.55	54.55
Gombe	*	*	*	*	*	*	*	*
Wamba	7.50	4.35	11.60	29.35	8.85	8.85	10.40	45.70
Lomako	*	*	*	*	*	*	*	*

Site	f tot	Party	Comm	DJ	Dens	Rain	Tmax	Tabmax
Mahale	69.93	13.40	80	*	5.70	1867.30	27.00	36.00
Okorobiko	*	9.90	*	1.50	*	2112.00	24.00	33.00
Kibale	45.45	5.80	44	*	2.20	1832.00	23.30	*
Gombe	*	4.00	57	*	2.50	2054.80	28.20	31.70
Wamba	54.30	16.90	66	7.00	1.70	953.00	30.00	32.60
Lomako	*	5.40	50	*	2.00	1903.10	27.30	32.00

Site	Tmin	Tabmin	m-m grm	m-f grm	f-f grm	grm-m	grm-f	grm-f-f
Mahale	19.00	16.00	97.00	63.00	7.00	45.90	79.70	10.00
Okorobiko	*	15.00	*	*	*	*	*	*
Kibale	16.20	*	28.00	24.00	26.00	41.90	37.70	28.00
Gombe	17.10	14.00	43.00	39.00	16.00	23.70	75.10	3.00
Wamba	17.10	12.70	27.00	103.00	48.00	82.90	61.70	36.00
Lomako	21.10	18.50	*	*	*	78.10	59.50	*

Site	grmf-m	grm-mm
Mahale	39.00	46.00
Okorobiko	*	*
Kibale	17.00	24.00
Gombe	9.00	29.00
Wamba	49.00	11.00
Lomako	*	*

4.4.2. Correlations between environmental and behavioural variables

As in chapter 3, the first step in developing multiple regression models, is to carefully examine the correlation matrices. Table 4.15 lists the significant spearman rank correlations for the behavioural data in table 4.13 (also see table 4.17). These correlations will serve as guidelines for stepwise regression models.

Table 4.15. Significant spearman rank correlations (r_s) between behavioural and environmental variables.

Behavioural variable	Dependent variable	r_s	N	P
Feed	Rest	-0.829	6	0.042
	Party	-0.812	6	0.050
	Community	-0.872	5	0.054
Move	*	*	*	*
Rest	Feed	-0.829	6	0.042
Day journey length	*	*	*	*
Home range	Density	-0.569	11	0.068
Density	Rainfall	0.566	11	0.070
Community size	Feed	-0.872	5	0.054
Party size	Rainfall	0.478	16	0.061

4.4.3. Determinants of the time budget

i. Data from table 4.13

During correspondence on the re-analysis of the baboon model of socioecology, between myself and J. Altmann and A. Bronikowski (also see Bronikowski & Altmann 1996), it emerged that different statistical packages resulted in different regression equations from the same original dataset. For this reason, regression equations were constructed from three computer programs; SPSS for DOS, SPSS for Windows, and a multiple regression program written in BASIC (source: R. Dunbar). The multiple regression program written in basic (from hereon referred to as MREG), built equations by examining the F-value between variables as they were added to the equation. The optimal number of independent variables is reached when the r-squared value no longer increases when further independent variables are added (see section 3.4.2.i.). Table 4.16. illustrates the results from the three different regression equations. The Windows and DOS versions of SPSS have identical F-value of inclusions (F-value to enter: 3.84; F-value to remove: 2.71). Therefore without further detailed knowledge of the underlying algorithm for

Table 4.16. Summary of equations derived from three different statistical programs.

(A) SPSS for Windows	(B) SPSS for DOS	(C) Multiple Regression model
$\ln(F) = 4.9868 - 0.3227 \ln(DEN) - 0.6086 \ln(PARTY)$	$\ln(F) = 8.527 - 0.6959 \ln(PARTY)$	$\ln(F) = 4.8850 - 0.6744 \ln(PARTY) - 0.081\ln(DEN)$
$\ln(R/S) = 0.4377 + 0.4800 \ln(P)$	$\ln(R/S) = 0.5866 + 0.4085 \ln(P)$	$\ln(R/S) = 0.9092 + 0.3589 \ln(P) + 0.045 \ln(DEN)$
$\ln(M) = 0.48025 - 1.3467 \ln(Mo50)$	$\ln(M) = 4.8025 - 1.3417 \ln(Mo50)$	$\ln(M) = 2.9054 + 0.026 \ln(Mo50) - 0.049 \ln(T) + 0.0458 \ln(DEN)$
$\ln(DJ) = 2.8729 - 0.6349 \ln(HR)$	$\ln(DJ) = 2.9729 - 0.6349 \ln(HR)$	$\ln(DJ) = 2.8792 - 0.6349 \ln(HR)$
$\ln(PARTY) = 6.6049 - 1.3353 \ln(F)$	$\ln(PARTY) = 6.6049 - 1.3353 \ln(F)$	$\ln(PARTY) = -0.6106 + 1.082 \ln(P) - 0.0625 \ln(N)$
		or, $\ln(PARTY) = -8.1356 + 1.3229 \ln(P) - 0.0748 \ln(DEN)$
$\ln(DEN) = 0.3146 - 0.6671 \ln(HR) + 1.7268\ln(P)$	$\ln(DEN) = -0.5591 - 0.6842 \ln(HR) + 1.7701 \ln(P) - 3.0663 \ln(T)$	$\ln(DEN) = -18.925 + 0.2624 \ln(N) + 2.5338 \ln(P)$
$\ln(N) = 5.5013 + 9.1973 \ln(Z)$	$\ln(N) = 3.8678 + 0.3055 \ln(DEN)$	$\ln(N) = 4.4510 + 0.0927 \ln(T) + 5.22 \ln(Z)$
$\ln(HR) = - 0.6784 - 31.5667 \ln(Z)$	$\ln(HR) = 1.3912 - 347.9131 \ln(Z) + 167.8275 \ln(Z)^2$	$\ln(HR) = 3.6301 - 0.8326 \ln(DEN) - 0.094 \ln(Mo50)$

Key: *F* = % time feeding; *R/S* = % rest + time resting; *M* = % time moving; *DJ* = day journey length (km); *PARTY* = party size; *DEN* = density (chimps / km^2); *N* = community size; *HR* = home range (km^2); *P* = mean annual rainfall (mm); *Mo50* = number of months with <50mm rainfall; *Mo100* = number of months with <100mm rainfall; T = mean annual temperature (°C); *Z* = Simpson's index of rainfall diversity; *DIV* = index of rainfall diversity.

Table 4.17. Database from which above equations are derived (see legend to table 4.13. for key to column headings).

Site	PARTY	DEN	N	HR	P	DIV	Z	P2T	T	Mo50	Mo100	F	M	R	DJ
Budongo	3.40	6.70	85	7.50	1919.00	0.76	0.89	*	21.00	*	*	*	*	*	*
Budongo	3.90	3.40	85	20.00	1919.00	0.76	0.89	*	21.00	1	3	*	*	*	*
Gombe	4.00	1.40	57	12.00	953.00	0.94	0.87	6	22.65	5	6	55.70	13.80	30.30	3.90
Mahale	6.20	4.30	80	15.00	1704.77	0.92	0.87	8	23.00	4	5	29.70	19.60	38.60	*
Bossou	6.00	4.50	23	6.00	1779.00	0.81	0.87	*	*	3	4	*	27.50	*	5.50
Okorobiko	9.90	*	*	*	2112.00	*	0.89	5	*	*	*	40.80	15.00	31.00	1.50
Assirik	4.00	0.09	25	300.00	1194.00	1.45	*	10	29.00	7	7	*	*	*	*
Tai	10.10	*	*	*	1534.00	0.67	0.78	12	24.00	1	3	*	*	*	*
Kibale	2.60	2.20	44	30.00	1383.70	0.57	0.90	12	19.75	0	5	62.00	15.00	33.00	*
Kibale	5.60	2.20	44	30.00	1383.70	0.57	0.92	*	19.75	0	5	*	*	*	*
Yalosidi	8.60	*	*	*	1869.00	0.59	0.92	12	*	1	3	*	*	*	*
Lomako	8.50	2.00	*	22.00	1903.10	0.45	0.91	12	24.25	0	1	*	*	*	*
Lomako	7.90	2.00	50	22.00	1903.20	0.45	0.91	12	24.25	0	1	*	*	*	*
Lomako	5.40	*	50	22.00	1903.10	0.45	0.91	12	24.25	0	1	*	*	*	*
Lomako	6.20	*	50	22.00	1903.10	0.45	0.91	12	24.25	0	1	40.40	16.10	38.00	2.40
Wamba	16.90	3.00	80	45.00	2211.00	0.41	0.92	12	23.55	0	0	18.00	13.00	43.00	*
Lope	2.40	0.23	*	*	1506.00	*	*	*	25.00	*	*	*	*	*	*
Kasakati	3.90	3.40	85	20.00	1919.00	0.76	0.89	*	21.00	*	*	*	*	*	*
Ugalla		0.08	725	250.00	984.00	0.97	0.89	*	*	6	6	*	*	*	*

stepwise regression used by the two versions of SPSS, there was no obvious explanation for the difference in the equations.

Feeding time in each of the three sets of equations (A to C) is related to chimpanzee density and party size (equations A & C). Resting time in all three equations is related positively with mean annual rainfall, with and additional positive influence of density in equation (C). Moving time is negatively related to the number of dry months, or seasonality of rainfall. The MREG program (C) introduced two further variables (temperature and density) to the moving time equation. Day journey length was negatively correlated with home-range size in all three equations. Two alternative equations were generated for party size (see table 4.18). Party size in equations (A) & (B) was negatively correlated with feeding time, reflecting the presence of party size in the feeding time equation. However, in equation (C), mean annual rainfall and group size (or density, in the alternative equation) entered the equation. Chimpanzee density was negatively related to home range size, and positively correlated with mean annual rainfall. Home range and temperature enter equation (B), and group size and temperature enter equation (C). The regression equation generated for group (community) size in each of the three models were different. Equation (A), positively correlated Simpson's index of rainfall diversity (*Z*), with community size, in equation (B) it was density, and in equation (C) temperature and *Z*. The equation for home range only differed for equation (C). *Mo50* (number of months with <50mm rainfall) entered equation (C), whereas *Z* entered equations (A) and (B). *Z* and *Mo50* may initially be considered to be similar, both describing the temporal distribution of rainfall. However *Z* and *Mo50* do not occur in the same principal component (fig. 2.12 and table 2.12). *Z* contributes to principal component 1, which included: latitude, rainfall, and P>2t (see legend to table 2.12). Whereas *Z* is in principal component 2, which also included DIV (index of rainfall diversity, see section 2.3.3). A quadratic function for *Z* was found to account for a greater proportion of the variance in the home range equation (B), than a linear equation.

Table 4.18. Step-wise regression analysis of chimpanzee data, using MREG program. All values logged.

De-pendent variable (x)	Inde-pendent variable (y)	sum of squares reduced	proportion of variance of y reduced	partial f (df)	cumulative sum of squares reduced	cumulative proportion reduced	multiple correlation coeffic-ient	F for analysis of variance (df)
Feed	Party	0.791	0.780	14.202(4)	0.791	0.708	0.883	14.20(1,4)
	Density	0.169	0.167	9.424(3)	0.959	0.947	0.973	26.76(2,3)
Equation:								
ln***F*** = 4.885 - 0.674 ln(***PARTY***) - 0.081 ln(***DEN***)								
Move	Mo50							
	Temp							
	Density				0.276	0.695	0.833	2.27(3,3)
Equation:								
ln***M*** = 2.905 + 0.029 ln(***Mo50***) - 0.0492 ln(***T***) + 0.046 ln(***DEN***)								
Rest/ Social	Rain	0.004	0.374	2.393(4)	0.036	0.063	0.612	2.39(1,4)
	Density	0.005	0.538	18.449(3)	0.085	0.912	0.995	15.64(2,3)
Equation:								
ln***R*** = 0.909 + 0.359 ln(***P***) + 4.504 ln(***DENS***)								
DJL	HR	0.341	0.981	52.61(1)	0.341	0.981	0.99	52.61(1,1)
Equation:								
ln***DJ*** = 2.873 - 0.635 ln(***HR***)								
HR	Density	11.63	0.814	35.24(8)	11.63	0.814	0.903	35.24(1,8)
	Mo50	0.763	0.0053	2.845(7)	12.396	0.868	0.932	23.10(2,7)
Equation:								
ln***HR*** = 3.63 - 0.833ln(***DEN***) - 0.094 ln(***Mo50***)								
Party	Rain	0.751	0.263	3.223(9)	0.751	0.264	0.513	3.223(1,9)
	Group	0.478	0.167	2.359(8)	1.229	0.431	0.657	3.03(2,8)
Equation:								
ln***PARTY*** = -6.10 + 1.081 ln(***P***) - 0.062 ln(***N***)								
Density								
Equation:								
ln***DEN*** = -18.925 + 0.262 ln(***N***) + 2.534 ln(***P***)								
Community								
	Temp	0.666	0.308	3.567(8)	0.667	0.308	0.555	3.56(1,8)
	Z	0.554	0.256	4.123(8)	1.220	0.565	0.751	4.54(2,7)
Equation:								
ln***N*** = 4.451 + 0.093 ln(***T***) + 5.220 ln(***Z***)								

Key: ***F*** = feeding time (%); ***M*** = moving time; ***R*** = resting/social time (%); ***DJL*** = day journey length; ***HR*** = home range size (km^2); ***PARTY*** = party size; ***DEN*** = density (animals/km^2); ***N*** = community size; ***P*** = mean annual rainfall (mm); ***Mo50*** = number of months with <50mm rainfall; ***T*** = mean annual temperature (°C); ***Z*** = Simpson's index of rainfall diversity.

To summarise, the regressions A to C (table 4.16) were qualitatively similar however, the consequences of the differences in intercept for predicting maximum ecologically tolerable group size will be investigated in section 4.5.

Having established that different statistical packages resulted in no real functional differences in time budget equations, SPSS for Windows was used to conduct step wise regressions on the following databases.

Table 4.19. Significant step-wise regression equations from data in table 4.17.

Equation	R^2	F (*df*)	*p*
ln(***F***) = 4.9868 - 0.3227 ln(***DEN***) - 0.6086 ln(***PARTY***)	0.999	7609.98 (2,1)	0.008
ln(***M***) = 4.8025 - 1.3467 ln(***Mo50***)	0.993	144.38 (1,1)	0.053
ln(***R/S***) = 0.4377 + 0.4300 ln(***P***)	0.951	39.16 (1,2)	0.025
ln(***DJ***) = 2.8729 - 0.6349 ln(***HR***)	0.981	52.61 (1,1)	0.087
ln(***PARTY***) = 6.6049 - 1.3353 ln(***F***)	0.929	39.38 (1,3)	0.008
ln(***DEN***) = 0.31458 - 0.6671 ln(***HR***)+ 1.7268 ln(***P***)- 3.282 ln(***T***)	0.763	29.02 (1,9)	0.004
ln(***N***) = 5.5013 + 9.1973 ln(***Z***)	0.940	30.97 (1,2)	0.031
ln(***HR***) = -0.6784 - 31.5667 ln(***Z***) - 0.7503 ln(***Mo50***)	0.905	19.08 (1,2)	0.049

All data natural logged (ln). ***PARTY*** = party size; ***DEN*** = chimpanzee density (animals / km^2); ***HR*** = home range (km^2); ***P*** = mean annual rainfall (mm); ***T*** = mean annual temperature (°C); ***Z*** = Simpson's index of rainfall diversity; ***F*** = feeding time (%); ***M*** = moving time (%); ***R/S*** = resting + social time (%).

Table 4.20. Significant step-wise multiple regression equations from data in table 4.13.

Regression equation	R^2	*F(df)*	*P*
ln(***F***) = 10.238 - 0.406 ln(***PARTY***) - 1.640 ln(***R***)	0.954	30.81 (2,3)	0.010
ln(***F***) = 4.853 - 0.696 ln(***PARTY***)	0.929	39.38 (1,3)	0.008
ln(***M***) no signficant equation			
ln(***R/S***) = 2.018 + 0.270 ln(***P***) - 0.114 ln(***F***)	0.997	341.13 (2,2)	0.003
ln(***R/S***) = 0.586 + 0.408 (***P***)	0.932	41.26 (1,3)	0.008
ln(***DJ***) = 2.87 - 0.635 ln(***HR***)	0.981	53.61 (1,1)	0.087
ln(***DJ***) = 2.00 - 0.051 ***HR***	0.998	493.42 (1,1)	0.029
ln(***PARTY***) = 6.604 - 1.335 ln(***F***)	0.929	39.38 (1,3)	0.008
ln(***DEN***) = - 0.559 - 0.684 ln(***HR***) + 1.770 ln(***P***) - 3.066 ln(***T***)	0.968	60.89 (3,6)	0.000
ln(***N***) = 3.868 + 0.303 ln(***DEN***)	0.758	25.04 (1,8)	0.000
HR = -142.29 - 12970.455 ln(***Z***) + 5733.40 ln(***Z***)^2	0.767	15.54 (2,10)	0.001
ln(***HR***) = 1.391 - 347.91 ln(***Z***) + 167.83 ln(***Z***)^2	0.531	5.67 (2,10)	0.023

See legend to table 4.19.

Table 4.21. Significant step-wise regression equations from data in table 4.14.

Regression equation	R^2	*F(df)*	*P*
ln(***F***) = 7.235 + 0.423 ln(***Unisex***) - 0.967 ln(***N***) - 0.126 ln(***GrFM***)	1.00	282790.3 (3,1)	0.001
ln(***M***) = -0.692 + 4.36 ln(***DJ***)			
ln(***R/S***) = 3.30 + 0.142 ln(***GrFm***) - 0.066 ln(***Mum***)	0.99	312.72 (2,2)	0.003
ln(***DJ***) = 43.92 - 1.76 ln(***T***)	0.99	456.33 (1,1)	0.029
ln(***PARTY***) = 223.193 - 39.91 ln(***Stem***)	0.99	1592.64 (1,1)	0.016
ln(***PARTY***) = 10.419 - 4.706 ln(***Bisex***)	0.82	22.15 (1,5)	0.005
ln(***PARTY***) = -0.02 + 0.609 ln(***GrFm***)	0.81	11.70 (1,5)	0.006
ln(***PARTY***) = -0.215 + 1.168 ln(***Mix***)	0.61	7.74 (1,5)	0.387
ln(***DEN***) = -31.741 - 1.335 ln(***F***)	0.75	12.25 (1,3)	0.024
ln(***N***) =			
ln(***HR***) = 4.32 - 0.555 ln(***Bisex***)	0.67	10.18 (1,5)	0.024

See legend to table 4.14.

Figure 4.9. illustrates the functional relationships between environmental and behavioural variables for the equations presented in table 4.19.

Figure 4.9. Flow diagram illustrating (causal) relationships between environmental and behavioural variables for chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) combined.

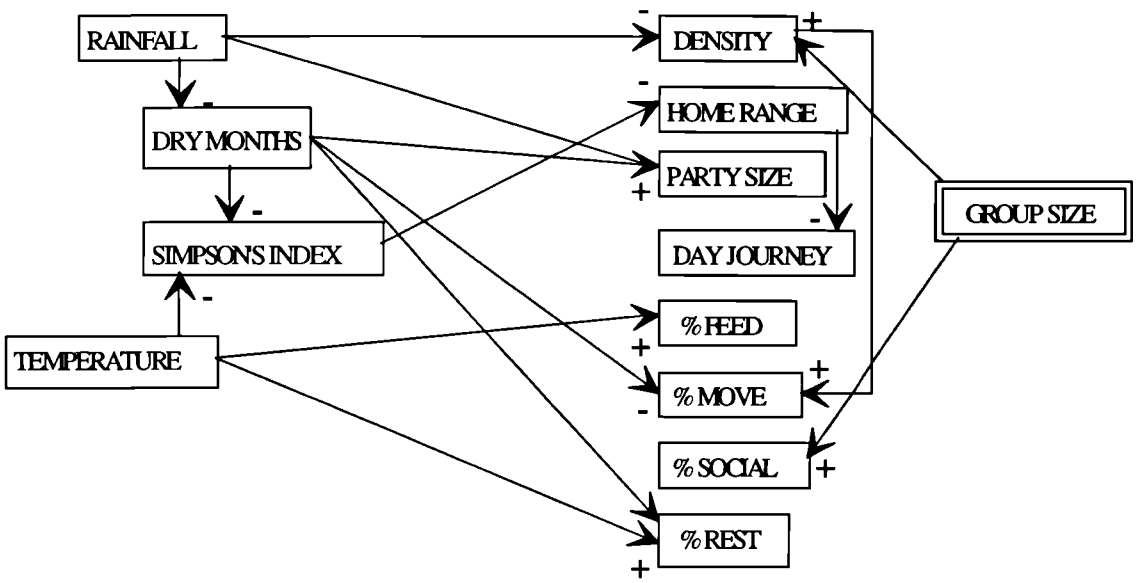


Figure 4.9 illustrates more graphically the functional relationships between behavioural and ecological variables in the model. As outlined in chapter 3 (section 3.4.2) caution must be exercised when interpreting the signs of regression coefficients in multiple regression equations, there fore the signs attached to the arrows in figure 4.9 should also be interpreted with caution.

I shall first discuss the equations in tables 4.19 and 4.20 which have comparable predictor variables. The difference between the databases is the larger sample of data on variables other than time budgets (group size, party size, density and home range size). The feeding time equation has similar predictors in the two tables (4.19 & 4.20). Where more than one equation is given for a dependent variable, the equation with the lowest *p*-value was selected as preferable for use in the model for predicting maximum ecologically tolerable group size (see section 4.4). A significant equation for moving

time equation could not be extracted from the data in table 4.13. Resting time in both tables 4.19 and 4.20 had mean annual rainfall as a predictor. The resting time equation in table 4.20 is more highly significant when feeding time was included as a predictor variable. Day journey length was positively correlated with home range size in both tables. However, unlogged home-range produced a more highly significant regression equation in table 4.20 ($\ln HR$: $r^2 = 0.981$, $p = 0.087$; HR: $r^2 = 0.998$, $p = 0.029$). The equation for party size was identical in both tables, feeding time only, entered the equation. This was because behavioural data were identical in the databases in both tables 4.13 and 4.17. The equation for chimpanzee density contained the same predictor variables in both tables, despite the ecological data being different in each dataset. The equation for density was therefore relatively robust to changes in input data. The equation for community size differed in the two tables; Z in table 4.19 and density in table 4.20. Finally, the equation for home range contained environmental predictors in both datasets; Z and Mo50. A quadratic function through Z best fitted the data in table 4.13., and similar to the equation for day journey length, home range produced a more significant equation when unlogged.

The equations in table 4.21. were based on a much smaller sample size (n = 6). Data were only selected for those field sites with time budget data. Because of the large number of variables, great care was taken when constructing multiple regression equations (see 3.2.1). Correlation matrices of the data were examined carefully before selecting candidate variables, to avoid the effect of collinearity among variables. Whilst there were small sample sizes, this additional data on party composition, grooming relationships and habitat quality was useful in further examining potential constraints on the main time budget categories. The equations generated in table 4.21. were descriptive, since their smaller sample sizes lessened the strength of the equations. As a consequence, these equations were not used to predict maximum ecologically tolerable chimpanzee group sizes.

The percentage of parties containing one sex and community size entered the equation for feeding time. This was similar to the equations in tables 4.19 and 4.20,

where party size entered the feeding time equation. Day journey length only, entered the moving time equation, however this equation only contains two data points, therefore a relationship between two points is inevitable. The resting time equation contained grooming relationships (*GrFm* = % grooming directed towards females) and party composition(*mum* = % parties containing mothers). Resting time includes social time (see section 4.3.3), therefore relationships between resting time and grooming relationships (i.e. social time) would be expected to appear as predictor variables. The equation for day journey length, and the first for party size contain too few cases (n = 2) to be discussed. Party size would be expected to be correlated with party composition (*Bisex* = % bisexual parties; *Mix* = % mixed sex parties). Party size was also positively correlated with the percentage of grooming bouts directed at females. Larger parties could be sustained, and a greater proportion of grooming directed at females. The greater the density of chimpanzees, the less the time spent feeding. It could be suggested the increased density increased feeding competition and reduced the time available overall for feeding. Home range size was negatively correlated with the percentage of bisexual groups (*Bisex*).

One further set of regression equations was generated, controlling for the influence of body size on feeding and moving time. The equations are outlined in the following section.

4.4.4. Body weight data for the chimpanzee model

In order to extend the time budget models on chimpanzees to the other species, including the early hominids, it is necessary to take body weight into account in the equations for feeding and moving time. Body weight will affect feeding time, through weight dependent energy requirements and gut-throughput rate. Body weight will determine stride length, and thereby influence the percentage time spent moving by the animal. By removing the effect of body weight, the amount of time animals *ought* to spend moving and feeding can be calculated. By removing the effect of body weight,

new body weights could be incorporated into the equations, allowing us to extend the models to other species (e.g. the early hominids).

The original regression analyses on baboons, and subsequently on chimpanzees, assumed that body weight was constant across the populations analysed. In the baboon model (Dunbar 1992*b*), body weights for specific field sites were not available, therefore equations based on a comparative study of the effect of rainfall on male and female body weight were used (Dunbar 1990). Mean adult body weight was a quadratic function of mean annual rainfall. Sex differences in body weight were more exaggerated in richer, versus poorer and intermediate habitats. The equation was used to determine body weight for each population, based on mean annual rainfall and temperature for that site. There is insufficient data on wild chimpanzee and bonobo body weights to quantify the relationship between body weight and environmental parameters.

Body weight may affect two of the activity categories; feeding and moving time. Larger animals have a longer stride length (Peters 1983) which would influence moving time. Feeding requirements are determined by two factors; (1) the absolute energy requirements of an animal, which scale 0.75 to the power of body weight (Kleiber 1961; Peters 1983); (2) larger guts have a slower throughput, therefore larger animals can extract a larger proportion of energy from ingested food. The observed time budgets are the times animals allocate to activity categories after they have compensated for the effects of their body weight. The raw data for feeding and moving times can be corrected for by the following two scalars:

$F_w = F \times W^{0.404}/B^{0.404}$

$M_w = M \times B^{0.333}/W^{0.333}$

Where F is the percentage of time spent feeding, M is the percentage of time spent resting, W the mean adult body weight of the target populations and B the mean adult body weight for the sample of populations from which the equations were derived. Throughput rate scales 0.346 to the power of body weight (Demment & van Sorest 1985). Combined, with the scalar for energy requirements (0.75), feeding time equals; 0.75 - 0.356 = 0.404 power of body weight (see Dunbar 1992*b*).

To adjust the feeding time equation for the effects of body weight, good estimates of chimpanzee body weight were required. Mean chimpanzee and bonobo body weights were used to adjust the equations for feeding and moving time. However, there is a paucity of data on wild chimpanzee weights, and those data that are available come from a limited number of field sites (tables 4.22).

Table 4.22. Mean body weights (kg ± SD) of adult common chimpanzees (*Pan troglodytes*) and adult pygmy chimpanzees (*Pan paniscus*). (adapted from Uehara & Nishida 1984).

Population	Adult males (1)	Adult females (2)	Weight ratio: (adult female / adult male × 100	Source
Pan troglodytes				
Mahale	42±5.4(n=6) range 34.3-49.6[3] 30.3-52.0[4]	35.2±3.9(n=8) range 30-41.8[3] 30-45.5[4]	83.8	Uehara & Nishida, 1984 (Dec 1973-Mar 1980)[6]
Gombe	39.5±4.5(n=9) range 33.6-47.3[3] 31.8-49.5[4]	29.8±2.2(n=6) range 26.4-32.3[3] 22.7-35.5[4]	75.4	Wrangham & Smuts, 1980[6]
	42.3(n=11)[7]	30(n=7)[7]	70.9	Pusey 1978 (July 1970-Dec 1975)[5]
E. Zaire	42.8±2.8(n=3) range 41-46	34.3±5.6(n=9) range 27.6-46	80.1	Rahm, 1967 (1963-66)[5]
Average of 3 populations	40.9±4.6(n=18) range 26.4-46	33.4±4.7(n=23) range 26.4-46	81.7	
Pan paniscus				
Lomako	45.0	33.2	73.8	Jungers & Susman 1984.

1) Differences between respective means are *not* significant
2) Differences between the means for Mahale and Gombe, and Eastern Zaire *are* significant
Mahale vs. Gombe: t=3.041, df=12, p<0.05
Gombe vs. E. Zaire t=3.513, df=13, p<0.01
Differences between means for Mahale and Zaire *not* significant.
3) Individual mean body weight
4) All measurements
5) Period in which measurements were taken
6) Statistical analysis of present paper, based on data from Wrangham & Smutts (1980)
7) Means were calculated by taking the second heaviest weight for each individual

A mean weight (mean of males and females) of 38.1 kg was used for chimpanzees, and 39.1 kg for bonobos (overall mean 38.6 kg). Chimpanzees and bonobos were considered together in the analysis for reasons outlined in section 4.3.1. The raw time

budget data in table 4.12 was adjusted for the effects of body weight, and stepwise regression equations set through the data (table 4.23).

Table 4.23. Feeding and moving time equations adjusted for body weight.

Regression equation	R^2	*F(df)*	*P*
$\ln(F) = 4.852 - 0.695 \ln(PARTY)$	0.96	39.38(1,3)	0.0082
$\ln(F_w) = 4.859 - 0.696 \ln(PARTY)$	0.97	40.70(1,3)	0.0078
$\ln(M)$ = *			
$\ln(M_w)$ = *			

* no significant equation.

4.4.5. Discussion

i. Determinants of the time budget

In this section I will review the time budget equations generated above, in the context of chimpanzee socioecology.

Wrangham (1979, 1986) has argued that feeding competition forces large parties to disperse when food patches become smaller, for example in the non-fruiting season Evidence for this was given by the fact that time spent feeding correlates negatively with party size. This claim is supported by two further field studies (see Bygott 1974; Wrangham & Smuts 1980). Feeding time in groups, as opposed to feeding time alone could be influenced by competing activities present when in groups (e.g. mating).

Animals must forage over an area that meets their energetic and nutritional requirements. Increases in group size require an increased travel area to find sufficient food (Terborgh 1983; Chapman 1990). Therefore animals are expected to travel further and expend more energy in a larger group. Group size itself is affected by the increased travel costs associated with the addition of new group members. Day journey length was found to be negatively correlated with home range size. The larger the home range area, the shorter the day journey length.

In primates there seems to be an inverse relationship between the time spent resting and time spent in social activity, where the complexity of social organisation depends on the time available to service social relationships. Species that are committed by their digestive strategy to spending a great deal of time resting may find the extent to which they can evolve complex societies limited by the amount of time they can devote

to social interaction. The time budget data available on chimpanzees did not allow a distinction between resting and social time due to an inconsistency in the definition and recording of time budget categories. In addition to the minimum time required for by animals for digesting, environmental conditions may impose constraints on the amount of time animals can remain active. This may be particularly significant in habitats with high ambient temperatures, where animals may have to rest in the shade in the hottest part of the day. Time spent resting is assumed to be time lost from the overall time budget, thereby shortening the overall length of the active day. With a shorter active day, the conflicts of priority between the remaining essential activities may become more acute. In extreme cases, the constraints of time budgets may force animals to chose between reducing the amount of time spent in social activity and reducing group size (in order to reduce the amount of time spent moving). A reduction in time spent moving will also allow the animals to reduce their feeding time requirement by that fraction that would have been needed to fuel travel.

Time budget data were scarce for chimpanzees, therefore in the following section I shall discuss in more detail where data were lacking and possible compensations that could be made for this lack of data.

The time budget data in this chapter, and chapter 3 assumed that animals balance their time budgets over a 24 hour period. A period of 24 hours was initially selected by Dunbar (1992*b*) because of its convenience. Nevertheless, an animals' active day may not be constant, nor 24 hours. For example in chimpanzees, females wake earlier and nest earlier than males. A female's reproductive status affects her sleep-wake patterns (Wallis & Mattama 1993). Additionally there were found to be seasonal differences in the length of the active day. When data were divided into seasonal quarters, there were significant differences in subjects use of daylight (late wet season: 11hrs 38min; late dry season: 11hrs 56min) (Wallis & Mattama *op. cit.*). The more animals there were in a group, the earlier they would be expected to wake, and the later they nested. Females tend to travel in larger parties when in a cyclic reproductive state, therefore chimpanzee females produced an indirect seasonal influence on sleep / wake times. The possible

confounding effect of seasonal differences in the length of the photoperiod could be dismissed, since animals stayed awake longer during the late-wet season even though the dry-season photoperiod is shorter. Therefore, both seasonal and social conditions affect the activity patterns of chimpanzees. Whilst acknowledging these influential factors on chimpanzee activity patterns, a 24 hour active period was still considered in this chapter.

ii. Paucity of time budget data

The time budget data that were available were unevenly distributed among the different chimpanzee habitat types. Specifically, data were lacking on the hotter and drier chimpanzee field sites. This may be particularly important with respect to the modelling of early hominid behavioural ecology. The study of chimpanzees in hot, dry habitats has been thought to be important for modelling the behaviour of the early hominids in a referential framework (see section 1.1.2.i), (Kortlandt 1983*b*, 1984; Laporte & Zihlman 1983). Chimpanzees' adaptation to arid conditions may provide insights into the adaptations of early hominids to similar habitats. Furthermore, comparisons of chimpanzees across a variety of habitat types may shed light on the sources and functions of the variability in chimpanzee behavioural ecology and social structure (McGrew 1983; McGrew *et al.* 1981). However, without a dataset representing fully all the habitat types chimpanzees currently occupy we must be cautious in our interpretation of these equations. Data on the west African chimpanzees, for example at Filabanga and Kasakati, are scarce. Observation conditions at these two sights are restricted, therefore information on behaviour, diet and ranging is gained indirectly. These indirect sources of behavioural data include: faecal counts, nest counts and the location of vocalisations (Izawa & Itani 1966; Kawabe 1966; Suzuki 1966, 1969; Izawa 1970; Kano 1971; Hoppe-Dominik 1991).

iii. Sex differences in behaviour

The extent to which the costs of group living differs between males and females could potentially be investigated through time budgets. Since time budgets can be considered

as an estimate of how subjects spend energy (Marriot 1988), the costs of coexistence can be highlighted by gender differences in activity budgets. However, there were insufficient data on sex differences in time budgets (table 2.11), to examine this question quantitatively for the chimpanzees.

In primate species that live in cohesive *bisexual* groups, the size of a groups' home range, and its average day journey length depend on individuals' metabolic needs. Therefore food patch size and dispersion are related to group size (Clutton-Brock & Harvey 1977; Terborgh 1983; Dunbar 1988; Barton *et al.* 1992). In species where males live *singly*, or in all-male groups and fission-fusion social groups, male mating strategies will affect day journey lengths. Male-male competition for access to females (whether or not females are in groups or dispersed), or to attract females from groups will both influence male day journey length. Additionally, males may have longer day journey lengths than would be expected on the basis of nutritional requirements (e.g. pottos: Charles-Dominique 1977; orangutans: Galdikas 1979; pattas monkeys: Harding & Olson 1986; grey langurs: Newton 1992, and spider monkeys: McFarland-Symington 1988). The *variance* in party sizes that is not accounted for by the distribution and density of food resources, may be partly explained by the age / sex composition of the group (Chapman *et al.* 1994).

Sexual dimorphism will affect the cost of locomotion. In the highly sexually dimorphic orang-utans (*Pongo pygmaeus*), travel is costlier for large adult males for smaller adult females (van Schaik & van Hoof 1996). Chimpanzees are less sexually dimorphic; however there is still a sex difference in travel costs, since travel for mothers is costlier than for males (Hunt 1989). Mothers have the added burden of carrying an infant, and may therefore be responsible for slower moving rates for mothers (2.3 versus 2.8 feet per second, Hunt 1989). Females have relatively small home ranges, compared to males (Chapman & Wrangham 1993).

The observed sex differences in time budgets, day journey length, and costs of group membership, detailed above were not available in sufficient *comparable* detail between field sites to conduct a quantitative comparative analysis.

iv. Seasonal differences in time budgets

Data on seasonal differences in time budgets and day journey lengths only exist for the chimpanzee population at Gombe (Teleki 1977; Wrangham 1977). Goodall (1986) gives data on seasonal differences in feeding time data for Gombe only. Although the data were from different sources and study periods, the data could not be considered as independent data points for comparison, since the demographic structure of the population did not differ significantly between the two studies. Since there were only data on seasonal differences in time budgets for one field site, seasonal differences in time budgets could not be investigated in the same detail as the baboon model (Dunbar 1992*b*).

Reduced rainfall and increased solar radiation in the dry season increases plant fibre content and therefore reduces its digestibility (van Soest 1982). Longer feeding times in the dry season may partly be a consequence of reduced plant food digestibility (wedge-capped capuchins (*Cebus ouvaceus*): Robinson 1986; baboons (*Papio* spp.): Dunbar 1992*b*). Food scarcity in the dry season may promote one of two responses; a decrease in energy expenditure (shorter day journey lengths), or an increase in energy expenditure seeking out scarce resources (increased feeding time) (Foley 1987). Because of the constraints of plant food digestibility in the dry season, daily energy requirements determine foraging time in the dry season, whereas digestive capacity determines foraging time in the wet season. Because of the constraints on foraging in the dry season, dry season feeding time may limit an animals ability to colonise a particular habitat.

The chimpanzee data were insufficient to develop quantitative equations; however, qualitative observations could be made. The following table (table 2.24) lists all the seasonal time budget data available from the literature.

Table 4.24. Seasonal time budgets for the Gombe chimpanzees (data from Teleki 1977; cited in Teleki 1989 & Wrangham 1977).

Activity category	Time budget (%)						
	Diurnal[1] (15hr)	Diel[2] (24hr)	Dry season (no rains)	Wet season I (short rains)	Wet season II (long rains)	Mean time (%) (terrestrial)	Mean time (%) (arboreal)
Teleki (1977)							
Feed	42.8	27.1	44.4	44.0	40.2	38.7	61.3
Move	13.4	9.4	14.1	15.6	9.3	99.2	28.0
Rest	18.9	47.7	15.7	21.3	18.8	65.8	34.2
Social	24.9	15.8	25.8	19.1	31.7	84.5	15.5
*Wrangham (1977)**							
All activities	**	**	44.0	35.5	66.8	**	48.8
Feed	**	**	68.7	56.6	87.9	**	71.1
Rest /groom	**	**	7.5	13.5	62.9	**	28.0
Move	**	**	18.1	3.6	11.9	**	11.2

[1] Diurnal = time budgets averaged of 15 hour active period. [2] Diel = time budgets averaged over a 24 hour time period.
* Arboreal time budgets only. (June - October dry season; November - May wet season).
** No available data

The time budget data from Teleki (1977) provides data in the conventional four categories (feed, move, rest and social); however, Wrangham (1977) merges resting and grooming time into one activity category. Dry season day journey length was greater than wet season day journey length at Gombe (Goodall, 1986: *wet season* 1.05km; *dry season* 2.5km: Wrangham 1977; *wet season*: 3.7 *dry season* I 3.5km; *dry season* II 4.5km). Time spent feeding was lower in the dry season in both studies.

4.5. MODEL OUTPUT

4.5.1. Introduction

The functional time budget equations presented above were used as inputs for a model of chimpanzee maximum ecologically tolerable group size. The same modelling technique was used to that outlined in section 3.4.2.ii. An example of the QBASIC model used to predict maximum ecologically tolerable group size is listed in appendix III part 3. Two sets of equations were used to generate maximum ecologically tolerable group sizes. The first set of equations are those from table 4.19, which use the data presented in table 4.17. This set of equations are run through the model twice. Once with the three time budget categories (feed, move, rest/social) (run A), and once with the following time

budget categories (feed, move, rest/social and the equation for social time from Dunbar 1990: see section 3.6.2) (run B). The second set of equations used in the model were those generated in table 4.20 from the data in table 4.13 (run C).

For each run of the model, the following output parameters were recorded for each integer of rainfall and temperature: time budgets, maximum ecologically tolerable group size (N_{max}), home range size, day journey length, density and party size. The following section outlines the results from each run of the model. The maximum ecologically tolerable group sizes presented in tables 4.25.a. to c. below are community sizes, not the smaller less stable party size.

4.5.2. Results

Preliminary results from these models were published in Williamson (1996), and were referred to in Dunbar (1996). The following tables outline the maximum ecologically tolerable group sizes obtained from each of the three runs of the model.

Table 4.25.a. Maximum ecologically tolerable group size (run A).

Rain	Temperature (°C)							
(mm)	**0**	**5**	**10**	**15**	**20**	**25**	**30**	**35**
100	0	0	0	0	0	0	0	0
300	0	0	0	0	0	0	0	0
500	0	0	0	0	0	0	0	0
700	0	0	0	0	0	5	989	0
900	0	0	0	0	152	357	503	0
1100	0	0	0	28	62	83	98	0
1300	0	0	0	11	16	20	22	0
1500	0	0	0	0	0	5	6	0
1700	0	0	0	0	0	0	0	0
1900	0	0	0	0	0	0	0	0
2100	0	0	0	0	0	0	0	0
2300	0	0	0	0	0	0	0	0
2500	0	0	0	0	0	0	0	0
2700	0	0	0	0	0	0	0	0
2900	0	0	0	0	0	0	0	0

Table 4.27.b. Maximum ecologically tolerable group size (run B).

Rain	Temperature (°C)							
(mm)	0	5	10	15	20	25	30	35
100	0	0	0	0	0	0	0	0
300	0	0	0	0	0	0	0	0
500	0	0	0	0	0	0	0	0
700	0	0	0	0	0	0	0	0
900	0	0	0	0	0	0	0	0
1100	0	0	0	0	31	66	85	0
1300	0	0	0	41	103	134	150	0
1500	0	0	0	99	161	191	205	0
1700	0	0	0	149	206	239	252	0
1900	0	0	0	192	245	280	293	0
2100	0	0	148	229	279	314	329	0
2300	0	0	185	263	310	342	361	0
2500	0	0	220	294	339	369	391	0
2700	0	0	253	324	366	395	417	0
2900	0	0	282	351	391	419	440	0

Table 4.27.c. Maximum ecologically tolerable group size (C).

Rain	Temperature (°C)							
(mm)	0	5	10	15	20	25	30	35
100	0	0	0	0	0	0	0	0
300	0	0	0	0	0	0	0	0
500	0	0	0	0	0	0	0	0
700	0	0	0	0	0	0	0	0
900	0	0	0	0	0	0	0	0
1100	0	0	0	0	0	0	0	0
1300	0	0	0	0	0	0	5	0
1500	0	0	0	0	0	78	93	0
1700	0	0	0	0	0	0	0	0
1900	0	0	0	0	0	0	0	0
2100	0	0	0	0	0	0	0	0
2300	0	0	0	0	0	0	0	0
2500	0	0	0	0	0	0	0	0
2700	0	0	0	0	0	0	0	0
2900	0	0	0	0	0	0	0	0

The equations using the data from table 4.17 (run A; table 4.25.a) predict maximum ecologically tolerable group sizes in the rainfall range 700-1500mm, and between 15 and 35°C mean temperature. By contrast the values for N_{max} in table 4.25.b. (run B) fall between 1100 and 2900mm rainfall and 10 and 30°C mean temperature.

The equations from run (C), predict values for N_{max} in a much more restricted habitat zone (1300 to 1500mm rainfall, and 25 to 30°C mean temperature). Where there was no significant equation for moving time in table 4.20, the equation for moving time

was used from the equation in table 4.19. Where there was a choice of equation in table 4.20, the most highly significant equation was selected for input into the model.

The model output for maximum N_{max}, party size, density, home range size, day journey length and time budgets for the equations in run (A) are illustrated in figures 4.10 a to f. Similarly to model output for run (B) are illustrated in figures 4.11 a to g. The data from table 4.25 were insufficient to warrant further presentation of the time-budget data.

4.5.3. Discussion

I shall begin by first discussing the model output for runs A to C in turn, before comparing the models. I shall then move on to a wider discussion on the accuracy of the models predictions.

Run (A)

Maximum ecologically tolerable group sizes were predicted to be extremely large in hotter, drier habitats. Whilst community sizes between 20 and 80 are usual (see table 4.17), the hotter and drier west African sites do in fact have larger community sizes (e.g. Ugalla, N = 725). Party sizes also increase with rainfall, reflecting the increase in resources in higher rainfall habitats which is able to meet a greater number of individuals' energetic requirements. In higher rainfall habitats party sizes may be sustained at lower temperatures than in lower rainfall habitats. This reflects the increased thermoregulatory constraints in drier habitats where there are fewer areas of shade for refuge. The model did not distinguish clearly between values for density at different rainfall values. The model was designed so that values for density were returned as integers. In addition the model did not seem to distinguish density in different habitat types despite the fact that mean annual rainfall was included as a predictor variable. Home range size was greatest at the lowest rainfall value that maximum ecologically tolerable group sizes could be sustained (700mm). Density at increasing rainfalls remained relatively constant, but required increasing temperatures for a value for density to be returned by the model. Lower mean annual rainfall indicated a poorer quality habitat, which required animals to

sustain a larger home range to meet their energetic and nutritional requirements. However, despite the larger home range in poorer quality habitats, animals had shorter day journey lengths. One explanation could be that on a daily basis chimpanzees forage in a small localised area rather than exploiting the whole of their home range.

Maximum ecologically tolerable group sizes could not be sustained at 700mm rainfall. As a consequence the time budget values for model run (A) (figure 4.10.f) at 700mm rainfall do not balance (sum to 100%) at 20 and 30°C. With increasing rainfall and increasing temperature, resting time increased, moving time remained constant and feeding time decreased. In higher rainfall habitats, food patch density could be assumed to richer, therefore animals would need to spend less time searching for food and would therefore have decreased feeding time. Time appeared to be taken out of feeding time for resting at higher temperatures (also see section 3.2.4). At higher temperatures greater time would need to be spent resting for thermoregulation.

Run (B)

The most obvious difference between runs A and B are the much larger values for N_{max} in run B. Group sizes were only sustained at much wetter habitats than run (A) of the model.

In this run of the model, the same equations were run as in run (A) with the social time equation replaced with that cited in Dunbar (1990) for the old world monkeys and apes (also see section 3.6.2). The definition of the time budget categories for the chimpanzee data differed between field studies; some merged social and resting time, others considered them as separate categories.

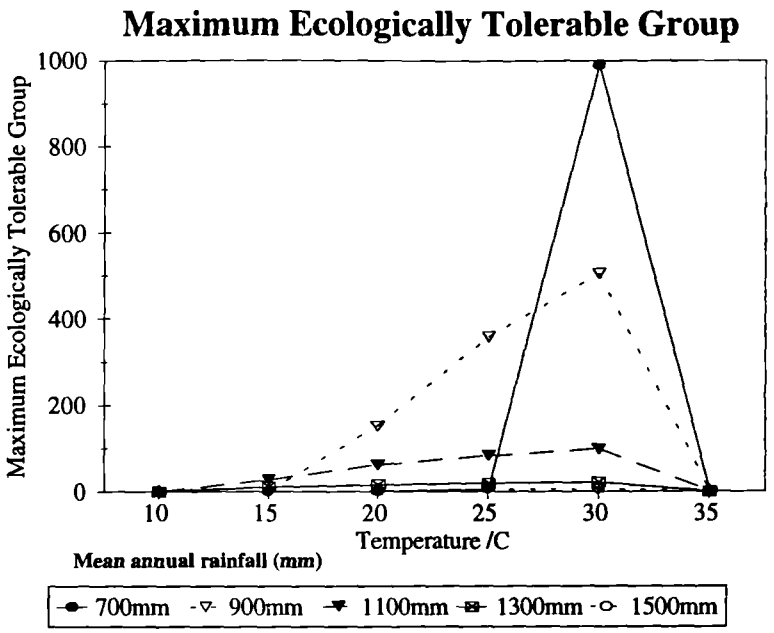
Despite the difference in magnitude of N_{max}, the trends in the remaining variables were identical to those in run (A).

Run (C)

The values for N_{max} were extremely restricted when the equations from table 4.20 were used as inputs for the model. The larger sample of party size and density should have improved the accuracy of the equations predicting these two variables. However, the model output only returned values in a very restricted habitat range.

Figure 4.10. Model output for run (A)

(A)



(B)

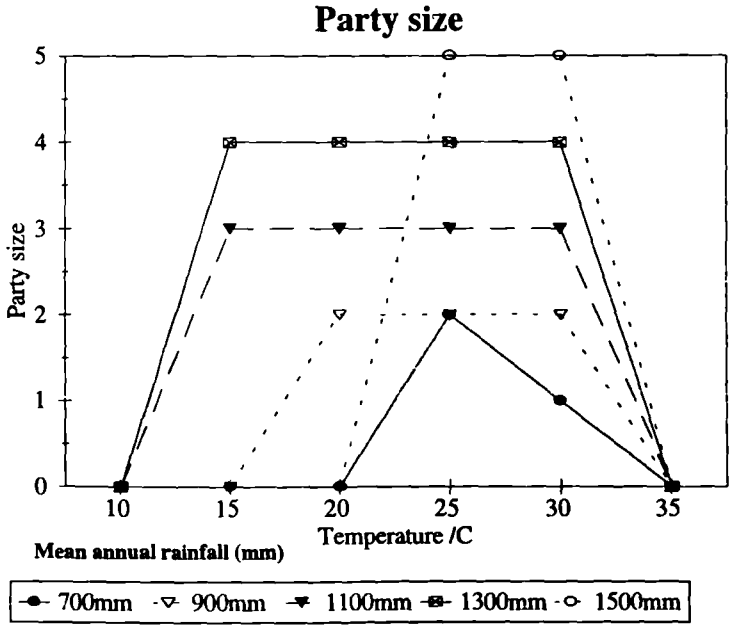
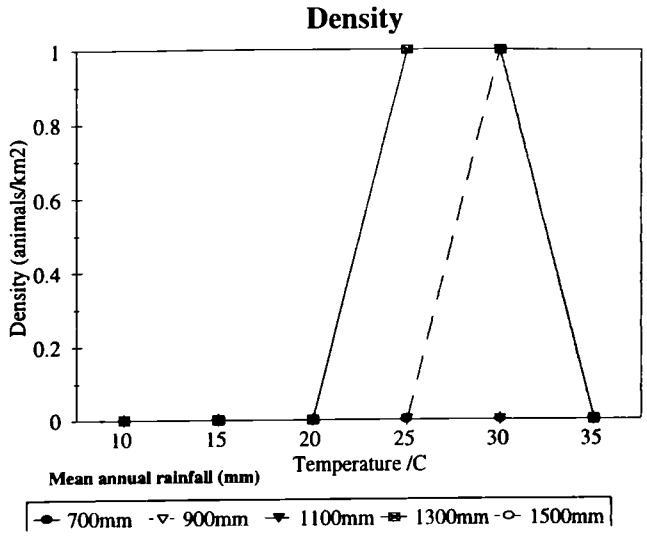
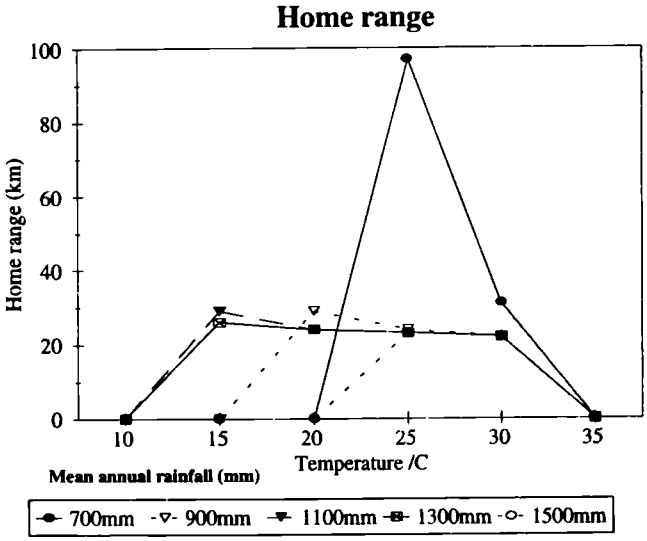


Figure 4.10. Model output for run (A)

(C)



(D)



(E)

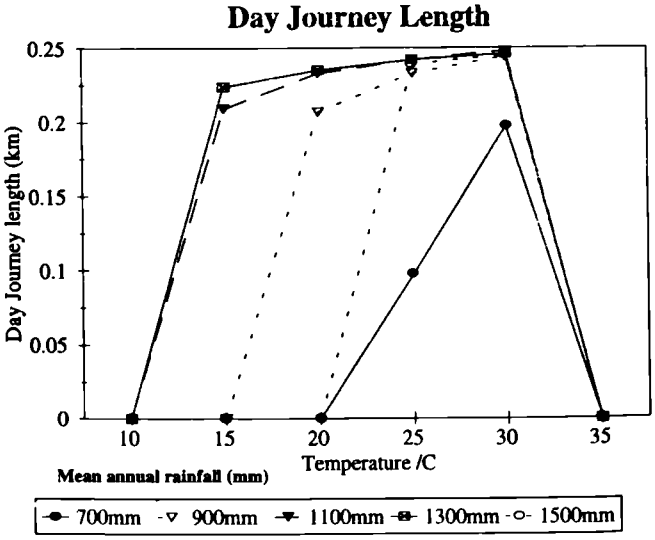


Figure 4.10.f Time budgets from maximum ecologically tolerable group size model (run A)

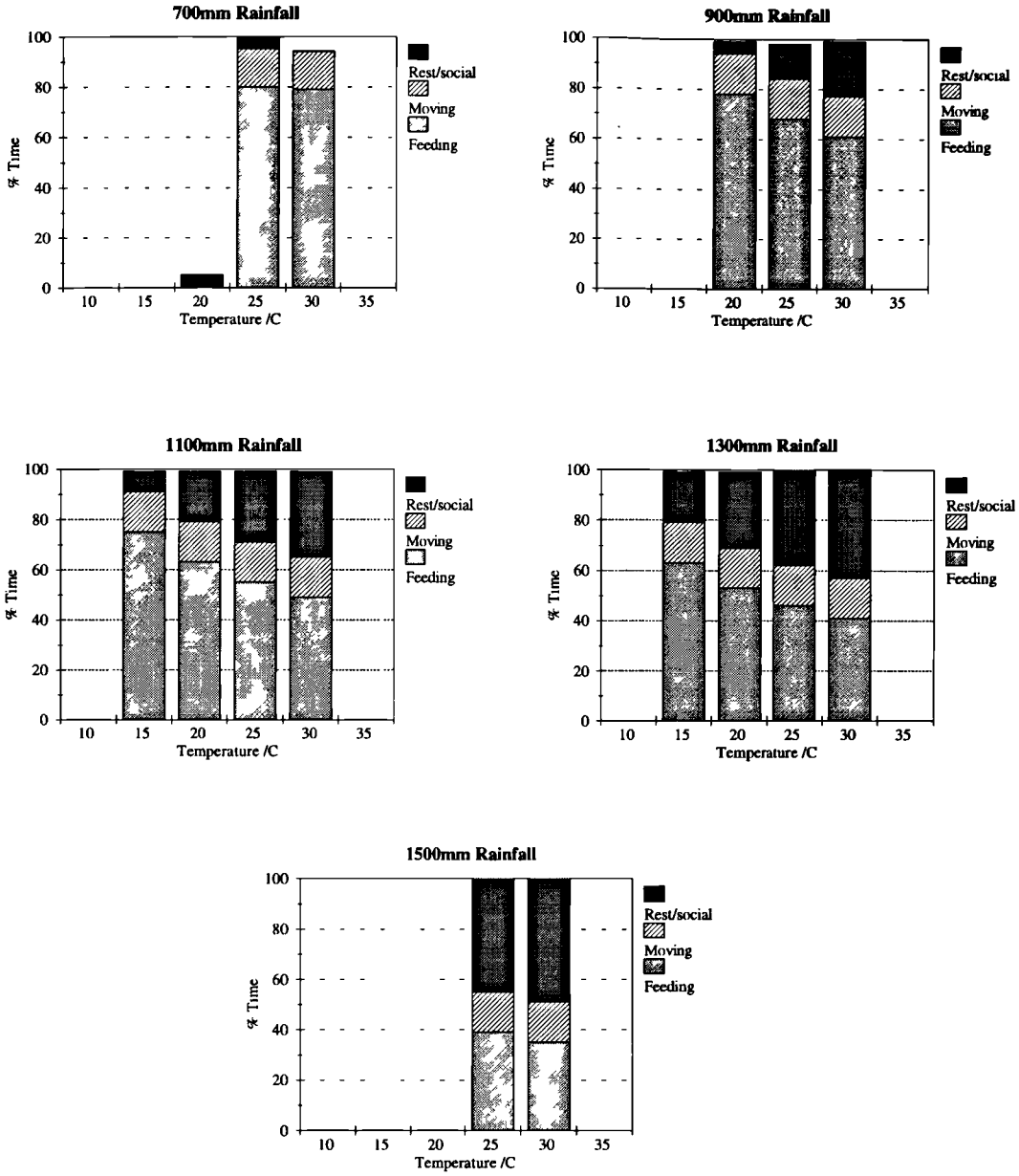


Figure 4.11. Output from maximum ecologically tolerable group size program (run B)

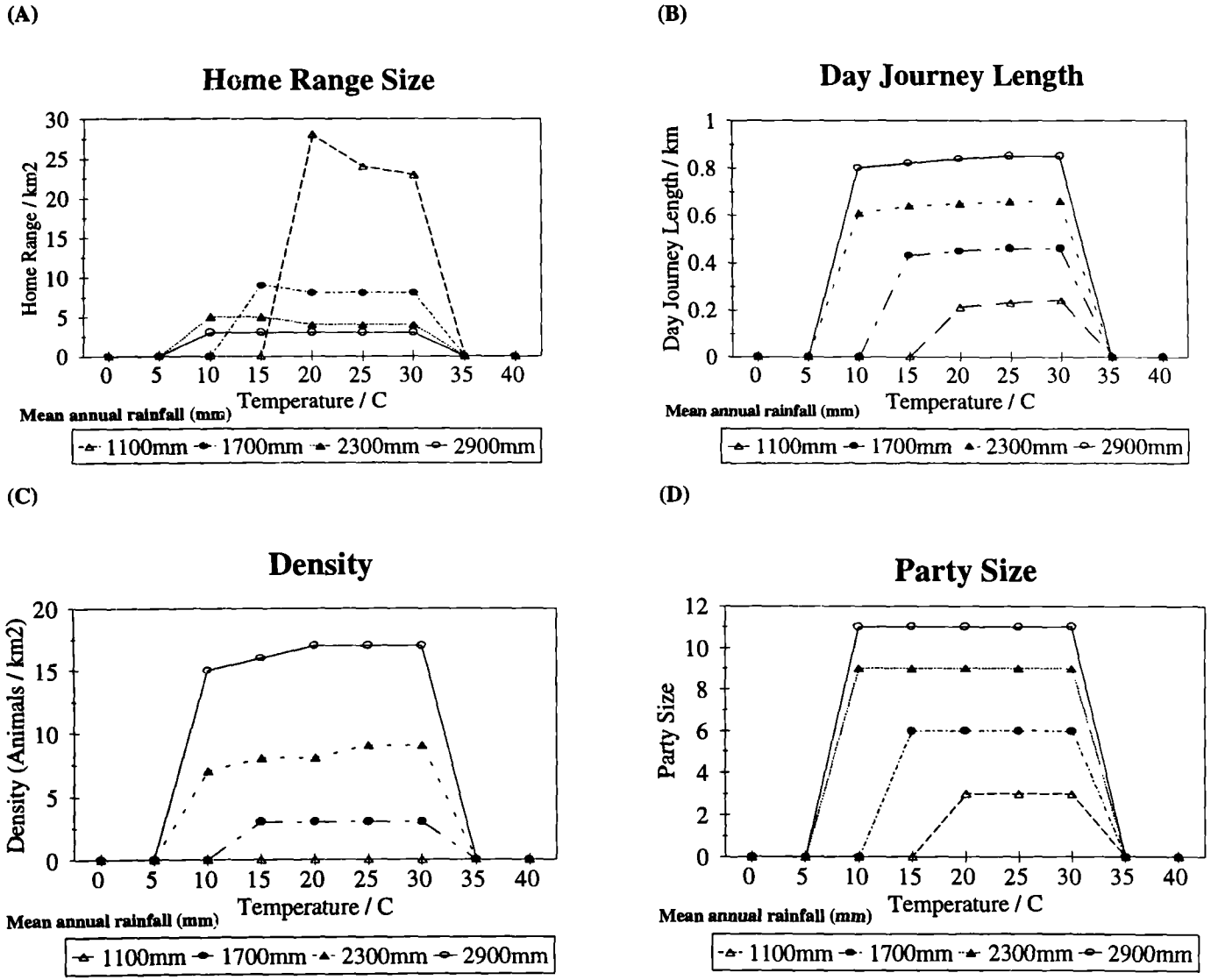


Figure 4.11. Output from maximum ecologically tolerable group size program (run B) (E)

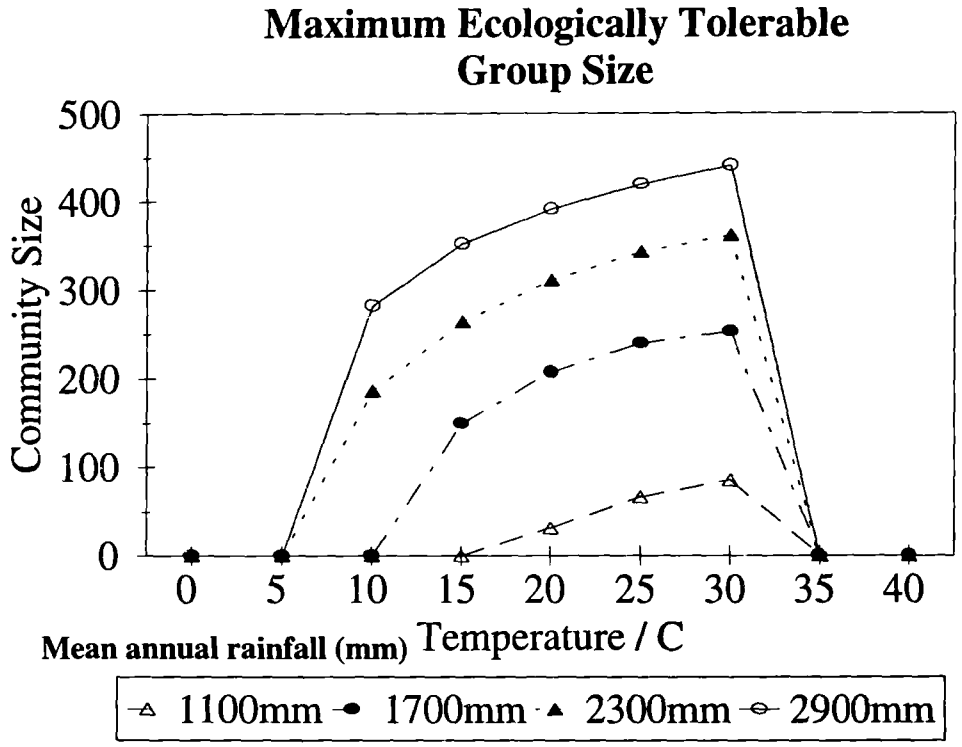


Figure 4.11.f. Time budgets from maximum ecologically tolerable group size model (run B)

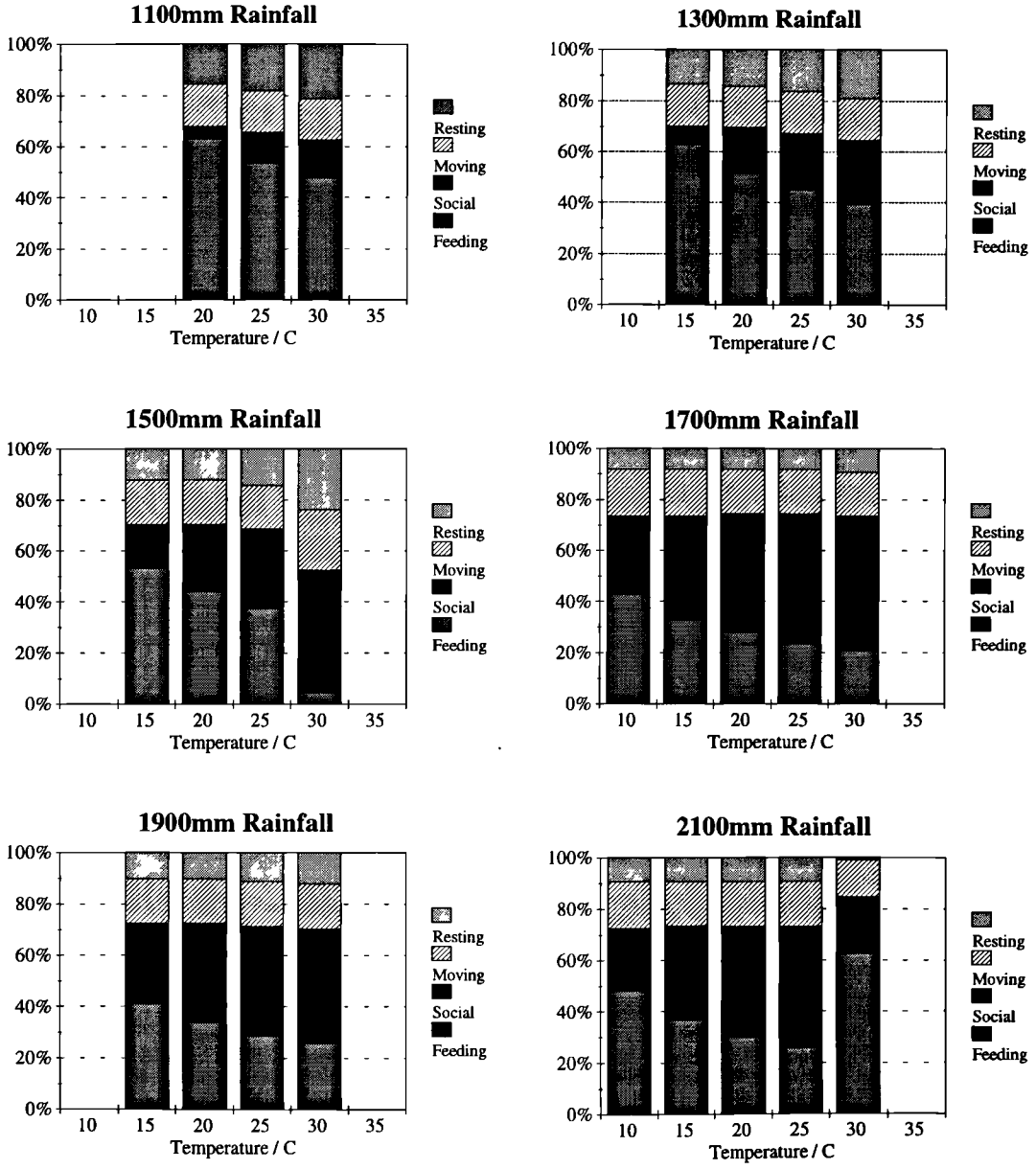
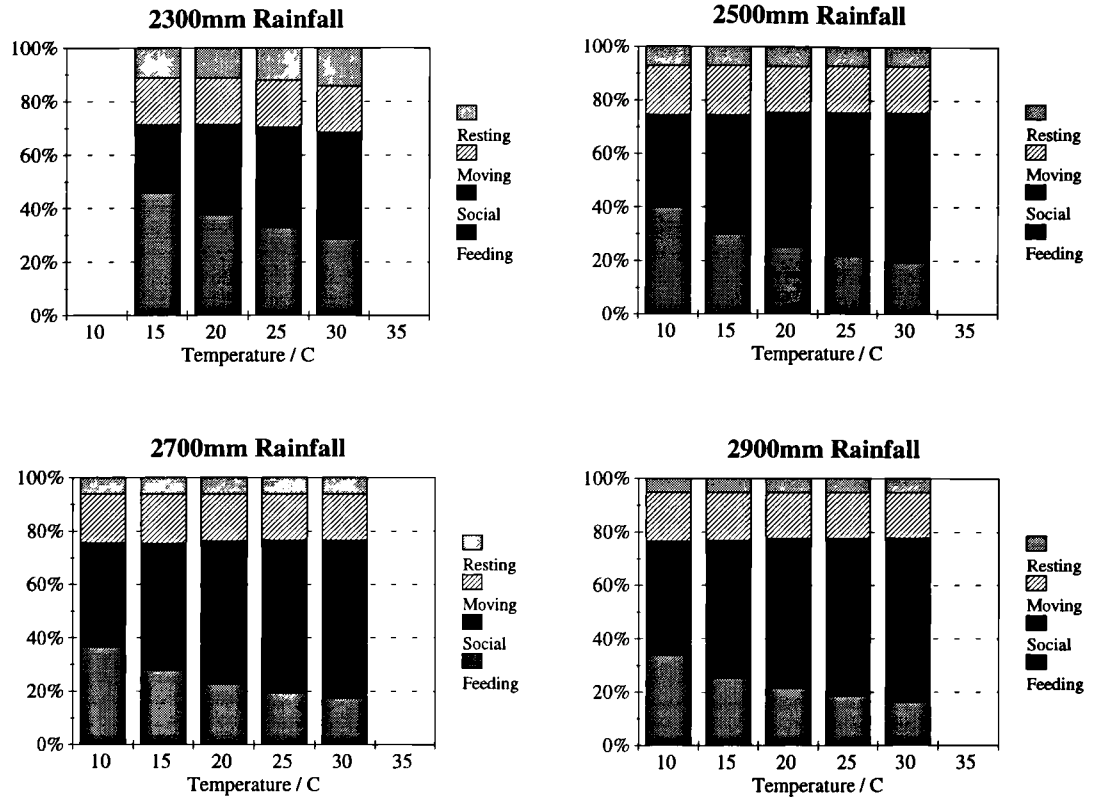


Figure 4.11.g. Time budgets from maximum ecologically tolerable group size model (run B)



The equations from run(A) at face value appear to predict most accurately the demographic and time budget variables of chimpanzees. However, unlike the baboon model (see chapter 3), there were insufficient time budget to allow for an independent subsidiary sample with which to test the results of the model. Therefore alternative means were sought for testing the results of the model

4.6. TESTING THE MODEL

4.6.1. Introduction

The equations from run (A) of the model were used to predict the geographical distribution of chimpanzees. The program used to predict maximum ecologically tolerable group size was rewritten so that the output values (N_{max}, density, day journey length, home range, party size and time budgets) could be predicted at specific values for environmental variables. The QBASIC model predicts N_{max} with the following climatic variables; *Mo50*, *Z*, *T*, *P* (number of months with <50mm rain, Simpson's index of rainfall diversity, mean annual temperature and mean annual rainfall respectively). The model was designed so that values of *Mo50*, *Z*, *T* and *P* could be used as inputs, and the model would predict N_{max} for those values.

Climate data from 70 weather stations were selected at random from the Wernstedt (1972) database (see section 2.4.3). Values of N_{max} were then predicted for each of these 70 sites using the equations from model (B) to test whether maximum ecologically tolerable group sizes could be sustained in those habitats. Figure 4.12.a. illustrates which of the 70 sub-Saharan data points could sustain chimpanzee group sizes, and which sites could not.

4.6.2. Geographic distribution of chimpanzees

Chimpanzees were predicted to live in the geographic regions where chimpanzees are currently found ($\chi^2 = 12.451$; df = 1; $p<0.01$). Refer to the map of current chimpanzee distribution (fig 4.12.b) for comparison. However, the model also predicted chimpanzees to exist in areas outside their current distribution. These occurrences could

be explained by a variety of factors. Habitat conditions present today in Madagascar may be suitable for supporting chimpanzee populations. However, the separation of Madagascar from mainland Africa around 120mya precluded its colonisation by chimpanzees. Those areas in Southeast Africa, where chimpanzees are predicted in areas outside their current distribution are mainly upland forest areas separated from surrounding areas by dryland savanna. Chimpanzees were also predicted by the model to exist in areas along the Great Rift Valley. Local variations in topography along the zone of the Great Rift Valley create local areas, sufficiently wet to support forests suitable for chimpanzees. However, the dynamic nature of the rift valley's geological history has meant that either these environments are too ephemeral or have remained isolated through time to support chimpanzees. There are reports of chimpanzees, or similar primates in this area in the recent past (see Huevelmans 1965) in Tanzania and Mozambique.

There is no fossil evidence of *Pan* or any of its direct ancestors at the time of the australopithecines, despite their proposed molecular similarity, and hence relatedness. Chimpanzees and gorillas are distributed in Africa in all the major forested regions, however these forested regions stop at the Great Rift Valley in eastern Africa. Vegetation and climate vary dramatically on either side of the rift valley. Wet western woodlands give way to drier eastern grasslands. The ecological conditions either side of the rift valley present today reflect ecological differences which arose 8 million years ago (mya). Chimpanzees are only distributed to the west, whereas hominid fossils are found only to the east. Furthermore Coppens (1994) proposes that the hominids and panidae have never occupied the same geographic area in their evolutionary histories. It was hypothesised that before hominidae and panidae separated, the rift valley did not constitute a sufficient barrier to divide equatorial Africa into distinct habitat zones. The rift valley was created approximately 8mya during a tectonic movement. The rift valley became a barrier, potentially disturbing the circulation of air, and hence weather patterns. As a consequence of the change in climatic conditions due to the uplift of the rift valley, air masses to the west maintained high precipitation due to the Atlantic ocean, and

supported forest vegetation. Whereas air masses to the east became organised into a seasonal monsoonal climate. This hypothesis has become known as the "east-side story" (Coppens 1994).

Pan paniscus only occur in the central Zaire basin, south of the Zaire river. There are thought to be no bonobos north of the Zaire river, and they do not have a natural habitat there (Kano 1992). Bonobo distribution is thought to be bounded by the Kasai / Sankuru rivers to the south, and the Lomami river to the east (Coolidge 1933; Kano 1984; van den Audenaerde 1984). In the Southeast of the Zaire basin no large rivers exist to provide boundaries to bonobo distribution, instead it is thought that a change in vegetation from rainforest to savanna delimits the extent of their range (Thompson-Handler *et al.* 1995). There is currently no evidence that bonobos range north of 2° and south of 4°, east of 18° and west of 24°.

The percentage occupation of habitat types at bonobo study sites illustrates that bonobos are tolerant of a wide range of habitat types and habitat disturbance (table 4.26).

Table 4.26. Percentage of habitat types in bonobo study areas

Habitat type (%)	Wamba*	Lomako*	Lilunga**
mixed semi-deciduous and evergreen forest	44.30	85.10	0.0
old secondary forest	15.60	2.30	64.85
Swamp	21.90	12.60	5.52
Recently disturbed forest and cultivation	13.60	0.0	25.09

* White (1992*b*); ** Sabater-Pi & Veá (1990)

New discoveries of bonobos as far south as Yasa (21' 24°E, 03' 42°S), a woodland / savanna habitat, confirm that bonobos are more plastic in their habitat preferences than previously thought.

4.6.3. Discussion

The types of independent test that could be conducted on this model were limited because of the restricted amount of data. Nevertheless this simple test of the model fulfilled some of the criteria for a good model outlined in section 1.3. The functional

relationships in the model were not derived from a particularly large sample size, however these were all the data that were available. However, the map of the geographic distribution of maximum ecologically tolerable group size both confirm the current range of chimpanzees and make further biologically plausible predictions.

The analyses presented so far in this chapter have made two key assumptions: that group size is related to environmental variables, and that the simple environmental variables used accurately characterise chimpanzee habitats. In the following section I shall conduct a simple analysis relating chimpanzee sub-group size to environmental variables.

At the end of the chapter I shall discuss the results of the model of chimpanzee socioecology in the light of this analysis.

Chimpanzee Study Sites in Africa (redrawn from McGrew et al. 1993; XXII-XXIII).

Chimpanzee study sites in Africa

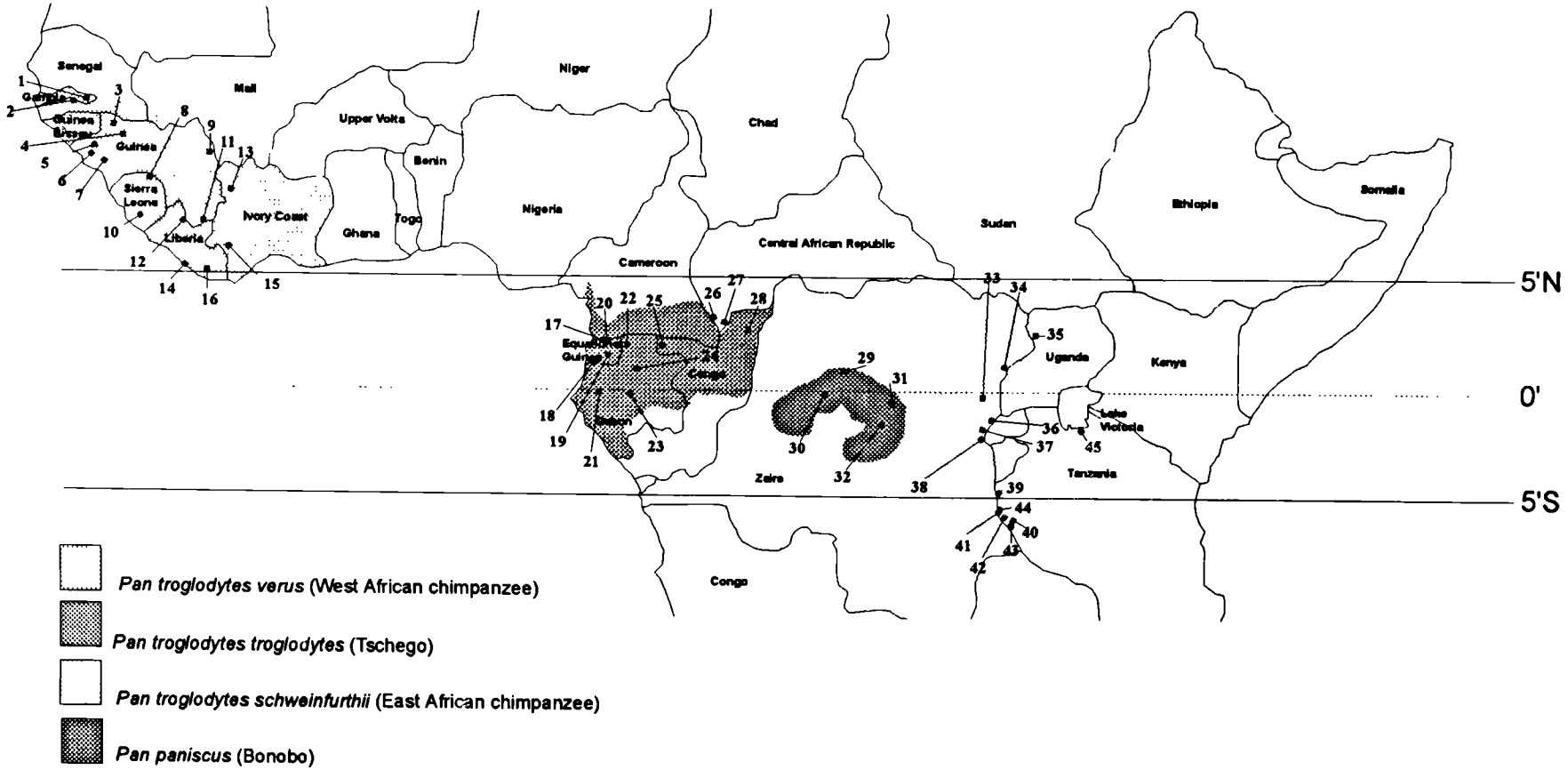
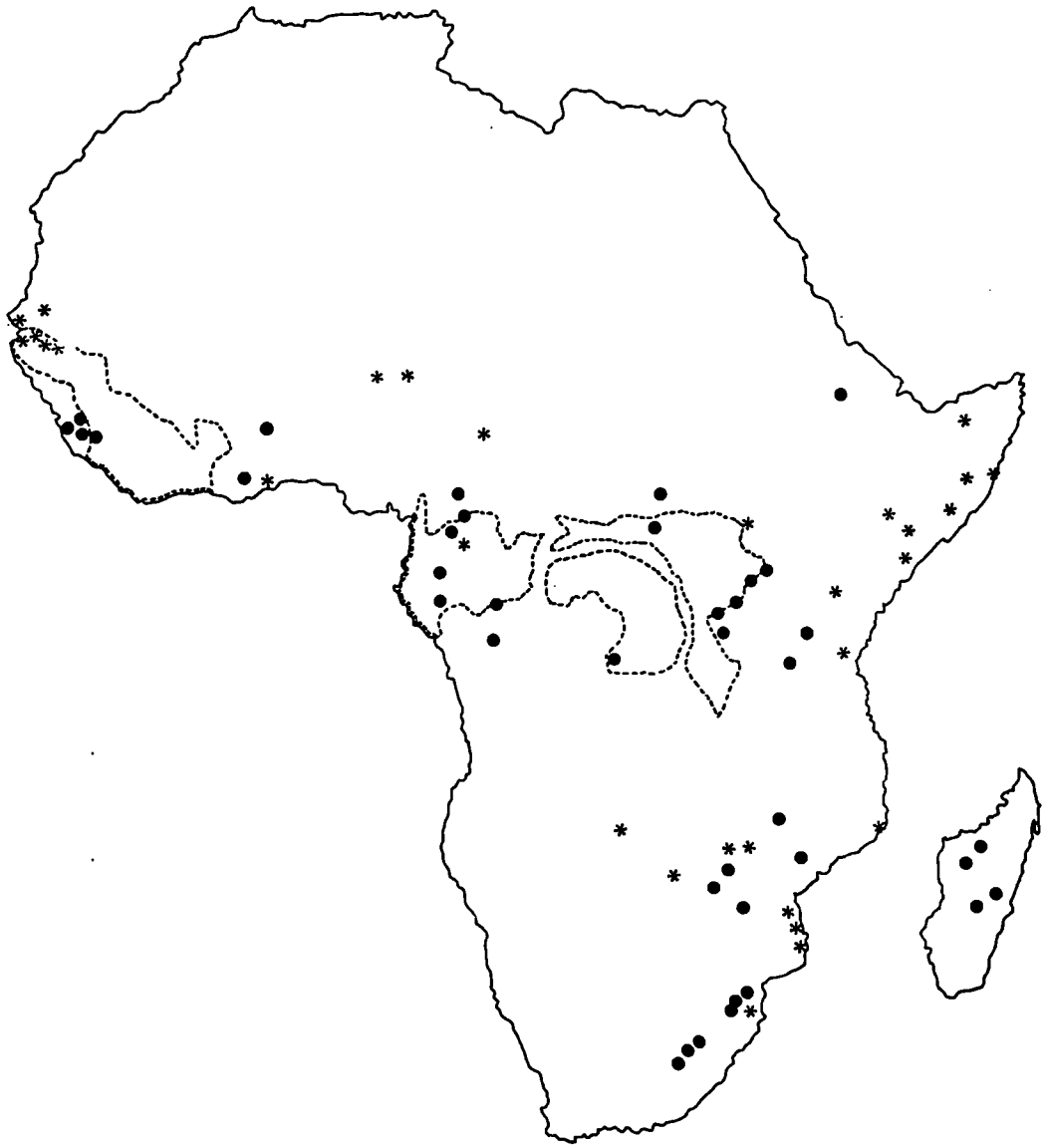


Figure 4.12. Map to illustrate whether or not chimpanzee group sizes could be sustained at specific weather stations in sub-saharan Africa



The present distribution of chimpanzees (*Pan troglodytes* and *Pan paniscus*) is delimited by dashed lines. Climatic data from weather stations from Wernstedt (1972) were used as inputs for the model. The full circles (•) represent weather stations where the model predicted that chimpanzees ***could*** exist, the stars (*) represent those sites where the model predicts that chimpanzees ***could not*** exist. Whether or not animals could exist in a geographic area was based on whether they could sustain groups given the environmental constraints on their time budgets.

4.7 CLIMATE AND CHIMPANZEE GROUP SIZE

4.7.1. Introduction

Having characterised chimpanzee habitats in climatic terms, I then related these simple environmental variables to chimpanzee party size. Models of primate group size (e.g. Terborgh 1983; Terborgh & Janson 1986) have generally assumed a non-linear relationship between group size and the costs of group membership. Intra-group competition increases with increasing group size (van Schaik 1983; Dunbar 1988; Isbell 1992). There is also a relationship between group size and the size of the feeding tree (Leighton 1993; Strier 1989; Chapman *et al.* 1994). In a comparison between chimpanzee and spider monkey sub-group sizes, both species were shown to rely on ripe fruit from depleting patches. This suggested that increased group size led to increased travel costs. The potential effects of intra-specific competition on group size were demonstrated by quantifying the relationship between seasonal variation in density and the distribution of food. If access to food required long travel distances, smaller group sizes would be optimal.

Much emphasis has been placed on the effects of environmental factors on party size. Environmental variables influence food distribution and quality, and therefore have an indirect effect on party size (White 1989; Southwick *et al.* 1991). The fission fusion social system is ideal for examining factors concerning group size, since subgroups frequently change size and composition (Chapman & Lefebvre 1990). Previous work has shown that chimpanzee subgroup size is influenced by ecological variables (e.g. patch size: White & Wrangham 1988; patch density: Wrangham *et al.* 1992; both: Chapman *et al.* 1994). The poorest fit between subgroup size and food resource size and density, was observed during periods of low food availability throughout the habitat. The observation of subgroup size tended to be biased towards times of the day when chimpanzees were in fig-trees, since it was difficult to find chimpanzees in the ground layer vegetation. This may bias the party size data presented in this chapter.

The distribution of food patches in space is thought to be important in determining party sizes. Time spent travelling at Gombe and Kibale remains fairly

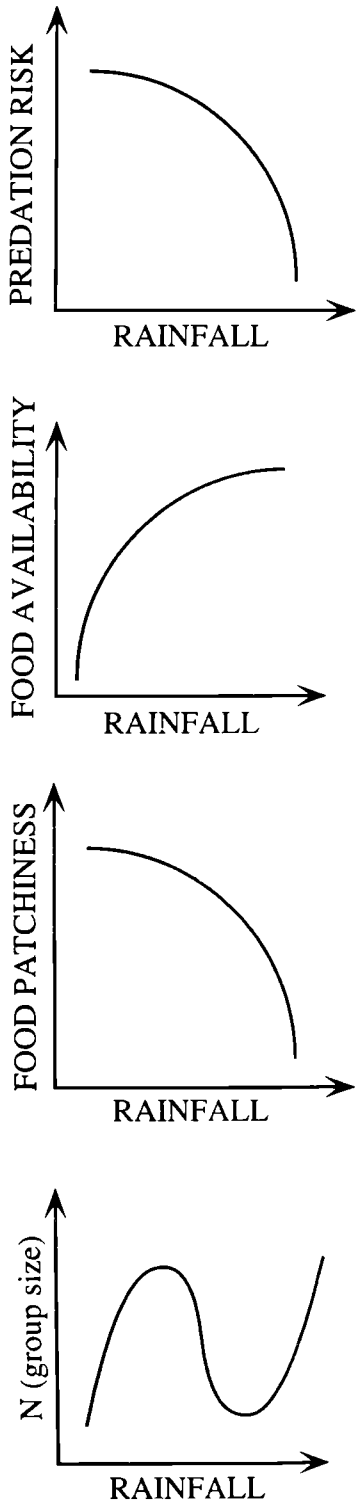
constant throughout the day, however chimpanzee density (an approximate measure of habitat quality) and party size at Kibale are smaller than at Gombe. From this evidence it could be inferred that in poor quality habitats, party size declines proportionately to avoid travel costs that would be incurred in large parties. Dispersion into smaller parties is only possible when predation risk can be reduced to a tolerable level. In well wooded habitats chimpanzees could afford to travel in groups of minimum ecologically tolerable size. It would be expected that party size would increase as the habitat became less wooded, despite the increased costs of travel between patchily distributed food sources. Therefore it chimpanzee and bonobo party size is related to aspects of the environment which may be indexed by simple climatic variables (see chapter 2).

Group size is thought to be determined by three primary variables (Dunbar 1988):

1. Food availability (indexed by rainfall) which determines the carrying capacity of the habitat, hence the maximum group size that habitat can sustain.
2. Predation risk, which determines the minimum permissible group size.
3. Food patch size, which imposes constraints on maximum group sizes.

The hypothesised relationships listed in 1-3 above may be related to rainfall, as illustrated in figure 4.13.

Figure 4.13. Hypothesised third order polynomial relationship between group size and rainfall.



Food availability increases with rainfall, whereas predation risk decreases with rainfall, because rainfall increases tree density which serve as refuges from predators. Finally patch size is positively related to forest volume, which in turn increases with rainfall (McGrew *et al.* 1981; Kortlandt 1983*b*). If the three relationships between rainfall and constraints on group size are combined, an 'N' shaped curve (or 3rd order polynomial) is expected between group size. It is predicted that a third order polynomial relationship should be found when group size is regressed against rainfall (for *Papio* baboons, see Dunbar 1988; fig 7.8: 136). This polynomial curve could theoretically be decomposed into its constituent parts, reflecting the relationship between rainfall and the three primary determinants of group size (see fig. 4.13).

Models of primate group size (e.g. Terborgh 1983; Terborgh & Janson 1986), have generally assumed a non-linear relationship between group size and the costs of group membership. However, despite this non-linear relationship between group size and environmental variables Dunbar (1988) emphasises that we should be cautious about attaching too much weight to the actual shape of the curve.

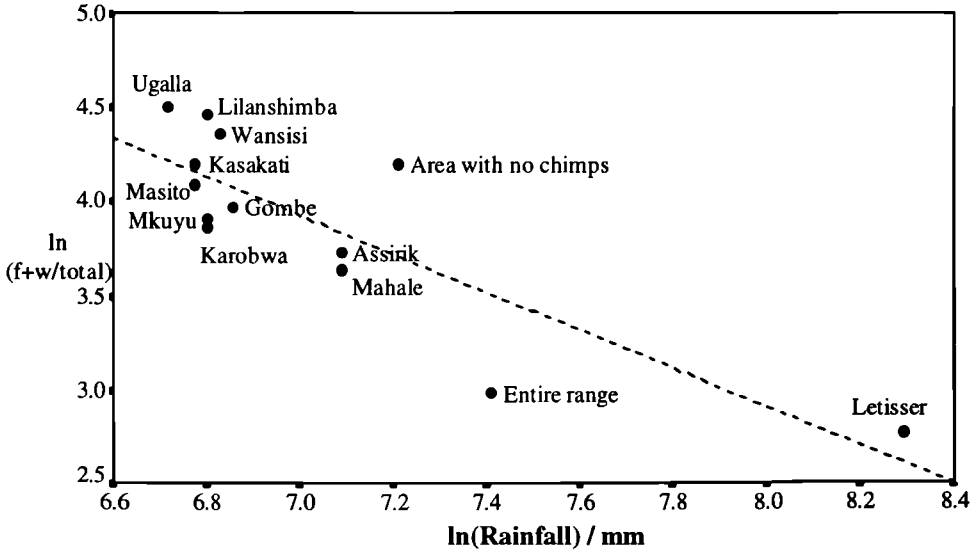
The hypothesised 'N'-shape distribution between rainfall and group size has been investigated for chimpanzees (Dunbar 1988; fig 13.2: 315). A 'J' shaped distribution was the result, when mean party size was plotted against mean annual rainfall for 7 chimpanzee and 2 bonobo field sites. In the following section I will first confirm that there is a relationship between forest cover and mean annual rainfall, and secondly re-run the regression analysis with more recently published party size data.

4.7.2. Rainfall indexes forest cover

Given the assumption that rainfall is a proxy for forest cover, I have used the data in Kortlandt (1983*b*) which tabulates data on forest and woodland cover as a percentage of the overall vegetation for chimpanzee habitats. This is the only source of *comparable* vegetation data on chimpanzee field sites, although it lacks data on bonobo field sites. These data update and correct those presented in McGrew *et al.* (1981). Figures 4.14 and 4.15. plot the data in table 4, pp. 267 (Kortlandt 1983*b*) (see table 4.27. for data). A

quantitative equation for the relationship between forest cover and mean annual rainfall could be calculated for the chimpanzee sites. A strongly negative regression equation was found between rainfall and forest cover ($\ln P$=13.973 - 1.44$\ln FW$, r^2=0.56, df=1,19, F=12.12, p=.006; where P = mean annual rainfall / mm, and FW = percent forest and woodland cover of the total vegetation). Similarly, a strongly negative relationship was found between mean annual rainfall and percentage woodland vegetation ($\ln Wood$ = - 0.359 + 9.33 $\ln P$, r^2=0.72, df = 1,11, F=11.56; p = 0.0059). This relationship is the reverse of that predicted by McGrew *et al.* (1981), who found that the higher the rainfall the greater the percentage forest cover. Kortlandt (1983*b*) accounts for the negative relationship by the fact that all the areas surveyed had suffered some degree of habitat disturbance and degradation. If this conclusion is correct, then we should be cautious about using direct climatic indices of habitat type for some of the chimpanzee field sites, where human

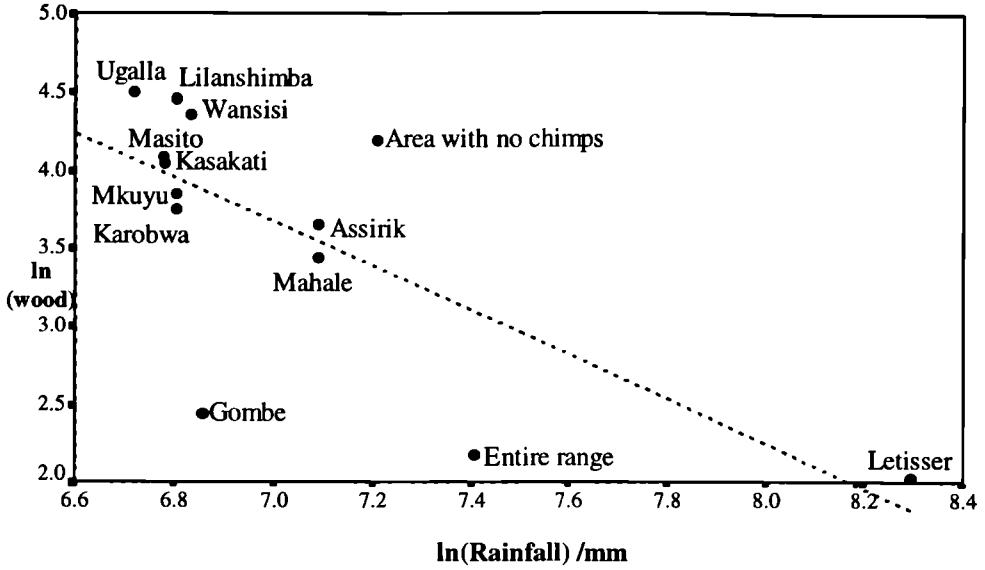
Figure 4.14. The relationship between mean annual rainfall and woodland and forest combined as a percentage of total vegetation. Data from Kortlandt (1983*b*: table 4, pp. 267).



$\ln FW$= -0.689 + 9.72 $\ln P$, (r^2=0.84, df=1,11, F=26.34 p=.0003) where P=mean annual rainfall (mm); FW=% forest + %woodland / total vegetation.
Sources: See Kortlandt (1983*b*) for locations of chimpanzee field sites. ***Rainfall:*** Entire, Assirik, Gombe (Kortlandt 1983*b*); Mahale, Wansisi, Lilanshimba, Kasakati, Masito, Karobwa, Ugalla (S.Uhehara, cited in Kortlandt (1983*b*), from Mahale short-term records). ***Vegetation:*** Forest (Kano

1972); Woodland (Kortlandt 1983*b*); Savanna (Kortlandt 1983*b*, measured from map in Wrangham 1977).

Figure 4.15. The relationship between mean annual rainfall and the percentage woodland cover in chimpanzee habitats. Data from Kortlandt (1983*b*; table 4, pp. 267).



ln***Wood***= -0.359 + 8.33 ln*P*, (r^2=0.72, df=1,11, F=11.56 p=.0059) where *P*=mean annual rainfall (mm); *Wood* = percentage woodland vegetation.

Table 4.27. Composition of vegetation (in surface percentages) at chimpanzee field sites in relation to long-term rainfall (Adapted from Table 4: 267, Kortlandt 1983*b*).

Area	Forest	Wood-land	Savanna (+agric)	F+W / F+W+S	Bamboo + Thicket	Grass	Swamp (+Beach)	Total	F+W / Total	Rainall
Letisser (1)	8.1*	7.7	79.6#	**17**	-	4.6#	-	100.0	**16**	>4000
Entire range	11.3*	8.9	65.5#	**31**	-	5.2#	-	90.9	**20**	(1400-1900)
Mahale(2)	10.1	31.5	26.6	**61**	22.4	15.3	4.3	110.0	**38**	1200(+)
Assirik (3)	3	39	27	**61**	3	28	-	100	**42**	1100-1300?
Gombe (4)	41.0	11.6	**		-	**	2.3	100.0	**53**	~950
Wansisi (2)	3.0	78.5	0.8	**99**	7.3	3.1	10.3	103.0	**79**	900-950
Lilanshimba (2)	2.9	86.8	13.2	**87**	-	-	-	102.9	**87**	850-950
Mkuyu (2)	5.1	47.5	51.2	**51**	-	-	1.3	105.1	**50**	900(-)
Kasa-kati (5)	8.4	58.9	14.4	**82**	2.7	15.7	-	100	**67**	850-900
Masito (5)	3.1	59.9	21.1	**75**	-	14.9	4.1	103.1	**60**	855-900
Karo-bwa (2)	9.6	42.7	13.6	**79**	20.0	19.7	4.0	109.6	**48**	850-950
Ugalla (2)	1.1	91.3	0.6	**98**	2.8	0.3	5.0	101.1	**91**	800-850
Areas without chimps.	0.0	66.7	5.9	**92**	15.5	5.8	6.1	100.0	**67**	800-1900+

* Including evergreen secondary bush; # Including some deciduous bush.; ** Savanna + Grass = 45.1%

Sources of vegetation data

1)This paper, section 8 (i). (2) Kano (1972). (3) This paper Table 3. (4) Measured by panimeter on the map in Wrangham (1977). (5) Suzuki (1969, p.109). Totals exceeding 100% are due to Kano's separate counting of riverine forest strips.

Sources of long-term rainfall data

(1), (3) and (4); This paper, Section 3, (i). (2) and (5): Mahale; short term records, S. Uehara (pers. comm). Other sites estimate by interpolation and from the topography (this paper and maps in Kano, 1972).

interference (e.g. agricultural activity and bush fires) has altered the natural vegetation structure.

Dunbar (1996) published equations relating tree and bush level cover for ten field sites in eastern Africa.

$$\ln B = -2.072 + 1.811 \ln T \qquad (r^2 = 0.36)$$

$$E = 86.28 - 14.078V \qquad (r^2 = 0.85)$$

where B is the percentage of ground covered by bush/shrub layer vegetation and E is the percentage of ground covered by tree layer vegetation, T = mean annual temperature (°C) and V = number of months with <50mm rainfall. This small sample size revealed rainfall seasonality to be an important predictor of the percentage of tree level cover in east African forested habitats. This is the only other published source of vegetation data related to climatic variables available for primate field sites, besides Kortlandt (1983) and McGrew *et al.* (1981). This highlights the need for more *comparable* ecological data from primate field sites, if we are to conduct more detailed quantitative analyses of primate socioecology.

4.7.3. Group size data

Chimpanzee and bonobo party size and community size data were collated from the literature. Rainfall data listed for each site are from table 4.9, from a mixture of study site sources and long-term weather compilations. Party size data is repeated for two chimpanzee sites (Budongo and Kibale) and one bonobo field site (Lomako). The two data points for Budongo may be justified on the grounds that a demographic change had occurred in the community between the two studies, similarly for the Lomako points. The two data points for Kibale represented two different communities in separate parts of the Kibale forest reserve (Ngogo and Kanywara). Potential biases to the party size data may occur from the definition of a party (see Chapman *et al.* 1993). Table 4.28. tabulates the definitions of parties for each field site to highlight this potential bias.

Table 4.28. Party and community sizes and mean annual rainfall for 12 chimpanzee and bonobo field sites.

Field site	party	community size	rain (mm)
Assirik	4.00	25.00	1194.00
Bossou	6.00	23.00	1779.00
Budongo[(a)]	4.40	85.00	1919.00
Budongo[(b)]	3.90	85.00	1919.00
Gombe	4.00	57.00	953.00
Kibale[(a)]	2.60	44.00	1383.70
Kibale[(b)]	5.60	44.00	1383.70
Mahale	6.20	80.00	1704.77
Okorobiko	9.90	*	2112.00
Taï	10.10	*	1534.00
Lomako[(a)]	8.50	*	1903.10
Lomako[(b)]	7.90	50.00	1903.10
Lomako[(c)]	5.40	50.00	1093.10
Lomako[(d)]	6.20	50.00	1903.10
Wamba	16.90	80.00	2211.00
Yalosidi	8.60	85.00	1869.00

* no data available

Party size data sources: ***Assirik***: Tutin *et al.* 1983; ***Bossou***: Sugiyama 1981; ***Budongo***(a): Sugiyama 1968; ***Budongo***(b): Reynolds & Reynolds 1965; ***Gombe***: Goodall 1968, 1986; ***Kibale***(a): (Ngogo) Ghiglieri, 1984, 1986[1]; ***Kibale***(b)[3]: (Kanywara) Clarke & Wrangham 1994; ***Mahale***: Nishida 1968[2]; ***Okorobiko***: Sabater-Pi 1979; ***Taï Forest***: Boesch 1991[4]; ***Lomako***(a): Kano 1983; ***Lomako*** (b): Badrian & Badrian 1984; ***Lomako*** (c): Malenky & Stiles 1994[5]; ***Lomako***(d): Chapman *et al* 1993[6]; ***Wamba***: Kuruda 1979; ***Yalosidi***: Kuruda 1979.

[1] Travelling parties from Ngogo site.
[2] Infants excluded.
[3] The mean party size of three different methods to estimate party size: initial party size plus all changes in composition, scans, "acoustic" party size (Clark & Wrangham 1993).
[4] From Boesch 1991, table 1, combined data from columns A, B & C.
[5] Party size = the average group size feeding on fruit and terrestrial herbaceous vegetation (THV).
[6] Party size calculated using first group sightings and changes in composition, as well as first sightings only.

Community size sources: ***Assirik***: Tutin *et al.* 1983; ***Bossou***: Sugiyama 1984; ***Budongo***: Suzuki 1969; ***Gombe***: Tutin *et al.* 1983; ***Kibale***: Wrangham 1986; ***Kibale***: Wrangham 1986; ***Mahale***: Kawanaka 1979; ***Okorobiko***: (no data); ***Taï Forest***: (no data); ***Lomako***: Malenky & Stiles (1994); ***Wamba***: Kano & Mulavwa 1984.

Rainfall sources: (see 4.9); name of weather station in brackets.
Assirik: Nicholson *et al* 1988 (Kolda); ***Bossou***: Nicholson *et al.* 1988 (Beyla); ***Budongo***: Uganda Dept. Meteorology; ***Gombe***: Tanzania Dept. Meteorology, 19231-60; ***Kibale***: Uganda Dept. Meteorology, 1963-72; Mahale: Takasaki *et al.* 1990 (Myako, 1976-84); ***Okorobiko***: Griffiths 1972 (cited in Moore 1992); ***Taï Forest***: Nicholson *et al.* 1988 (Soubré); ***Lomako***: Malenky 1990; ***Wamba***: Nicholson *et al.* 1988 (Befori); ***Yalosidi***: Nicholson *et al.* 1988 (Tshibanda, 1927-49).

4.7.4. Results

The correlation between community size and rainfall was non-significant (2-tailed r_s = 0.1941, n=13, p = 0.525), by contrast to the correlation between rainfall and party size which was significant (2-tailed r_s=0.59, n=13, p=0.016). Linear, quadratic (fig. 4.16) and cubic regressions (fig 4.17) were set through the data in table 4.28, and were found to be increasingly significant (see table 4.28). Whilst all the regression slopes are significant ($p < 0.02$) caution should be exercised in interpreting the cubic regression where the Taï Forest party size is high relative to mean annual rainfall. As discussed in section 4.2. the driest site was not Mount Assirik (as in Dunbar 1988; fig 13.2: 315), but Gombe. However, like Dunbar (1988), the wettest sites are Okorobiko and Wamba. The interpretation of the curve generated from the party size and rainfall data in Dunbar (1988), was considered to be one of four possibilities: (1) positive linear correlation; (2) no correlation; (3) a U-shaped relationship; (4) a J-shaped relationship (with a long-tail to the right). Some form of U-shaped relationship was found to be most significant.

Assuming increasing forest cover with increasing rainfall (but see figure 4.14; Kortlandt 1983*b*), the low party sizes at low mean annual rainfall could be accounted for by low predation risk. Increasing forestation, and improved habitat quality at high rainfalls, permit larger party sizes. The increased habitat quality does not *cause* the formation of larger party sizes but facilitates them. The two populations with the largest party sizes and wettest habitats (*Pan paniscus*: Wamba; *Pan troglodytes*: Okorobiko) feed much more heavily on herbage than other chimpanzee populations (Wrangham 1986). Bonobos may have dental adaptations to the greater proportion of herbage in their diet (Kinzey 1984).

Figure 4.16. Regressions of chimpanzee party size against rainfall (see table 4.28) for data.

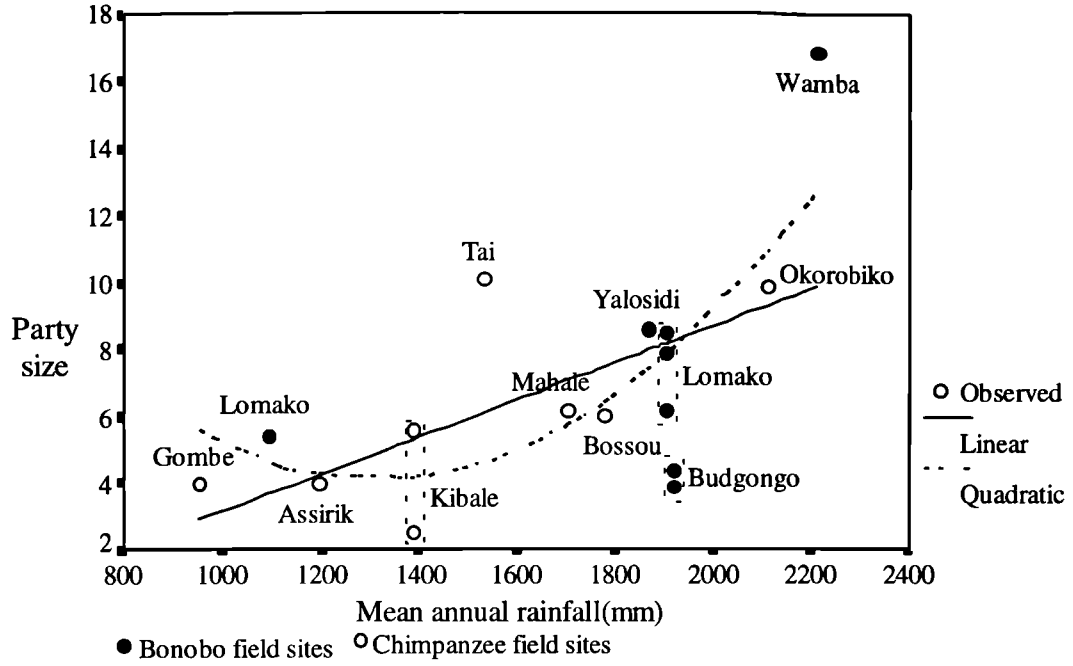
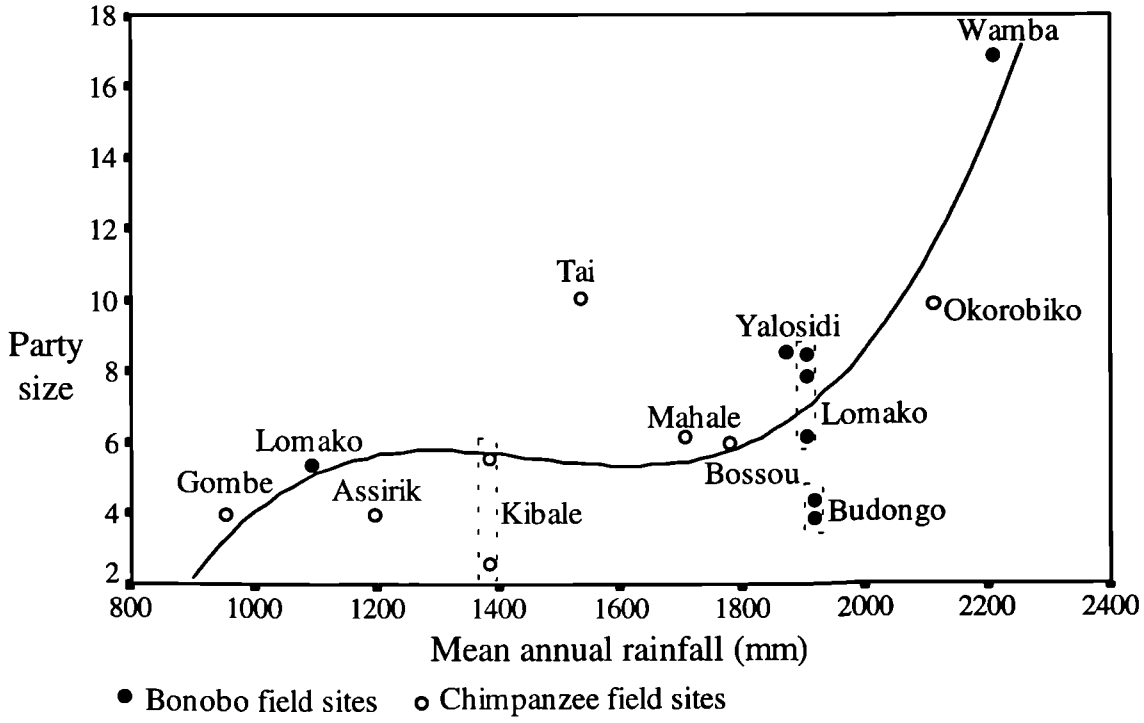


Table 4.29. Regression equations:

Equation	constant	rain	rain**2	rain **3	r^2	df	F	*p*
Linear	-2.360	0.006	-	-	.350	1,14	7.536	0.016
Quadratic	22.896	-0.284	1.080*10-5	-	.500	2,13	6.500	0.011
Cubic	9.938	17.376	-9.073**10-6	4.431*10-9	.538	2,13	7.563	0.007

Figure 4.17. Cubic regression of party size against mean annual rainfall. See table 4.28. for data.



Discussion

The natural variation in sub-groups (parties) in fission fusion societies, provides a basis for testing general ecological models of animal group size, since changes in subgroup size can be related to variation in ecological conditions. Existing comparisons of subgroup sizes among chimpanzees, and between chimpanzees and bonobos in different geographically isolated communities (Wrangham 1986; Nishida & Hiraiwa-Hasegawa 1987; White & Wrangham 1988) may be confounded by the definition of subgroups, and collection of data on subgroups in the field (Chapman *et al.* 1993). Three issues concerning the definition of subgroups are important. Firstly, the density of vegetation will affect observation conditions, therefore subgroup size may be more a consequence of observability than a direct correlation with habitat quality. A second issue concerns the duration of study, and hence habituation of the animals. Habituated animals are more likely to be included in counts of subgroups than less habituated animals. The third issue concerns the method used for locating subgroups in the field. Detailed account of the sources of party size data was made in table 4.28. to highlight the possible biases in party size data.

Support could not be found for the hypothesised polynomial relationship between group size and rainfall (fig. 4.13), nevertheless group size was not found to be a simple linear function of rainfall (habitat quality). The relationship between group size and rainfall is not unique to group living primates. Bighorn sheep in desert and mountain environments in six North American states, showed consistent group size fluctuations with varying plant productivity, indexed by mean annual rainfall (Berger 1988; $r^2=0.93$, $p<0.001$, fig. 1: 166). The graph of the results was interpreted to be 'J' shaped. This relationship demonstrated a relationship between inter- and intra-specific group size and underlying resource distribution. However this relationship says little about social systems or whether these social systems are directly shaped by either ecology or phylogeny (Berger 1988).

Theory predicts that large groups are favoured when resources occur in large clumps, distributed randomly in space and time. Small groups are favoured when food

patches are small and uniformly distributed. However, Rodman (1996) provides evidence from initial simulations, for the alternative; that uniformly distributed small patches favour large foraging groups. Rodman (1996) finds an 'N' shaped curve in forests where food is evenly distributed, where large groups feed more effectively than small groups. This result suggests alternative reasoning as to the function of large groups with respect to foraging efficiency, and could be relevant to the understanding of the social organisation of old and new-world monkeys. There is one important difference with Rodman's (1996) analysis, and that is that he considers only two variables; foraging efficiency and group size. The overall pattern of the graph in Rodman (1996) appears to show the same 'N' shaped curve predicted by Dunbar (1988), however there are differences. Mean group size is high at low rainfalls since fewer trees are available as refuges from predators. At higher rainfalls, large groups are optimal, because food patches are larger.

4.8. CONCLUSION

4.8.1. Introduction

The aim of this chapter was to extend the models developed on baboons and gelada (see section 3.3) to the another genera. The extension of the models to an ape species serves two purposes. Firstly to further verify the modelling technique and secondly to provide a basis for extending the model further to the early hominids. In this discussion I shall review the accuracy of the behavioural and environmental data that form the input variables for the model. I shall then discuss the results from the maximum group size model, and conclude with a general discussion on the relationships between ecological and group size variables.

4.8.2. Ecological data

The analyses in chapter 2 revealed that accurately sited climate data were more important than long-term climate data that were not close to the primate field site. With this in mind climate data were compiled from a combination of long- and short-term sources

emphasising the accuracy of proximity of the climate data. The compilation of accurately sited long-term climate data were used to characterise seasonality at each of the chimpanzee and bonobo field sites. The bonobo field sites were found to have the highest rainfall and lowest seasonality compared with chimpanzee field sites.

4.8.2. Time budgets

Between-site comparisons of chimpanzees were restricted due to the different criteria for behavioural observations. One case in point is party size, the definition of which varies greatly from site to site. Mitani & Nishida (1993) made some attempt at unifying the definition of party size, by an 'acoustic' definition. The different definitions used for recording time-budget categories restricted the number of data points available. Not all researchers had recorded separate categories for resting and social time, therefore the two categories were averaged and considered as one single category. Care was taken when compiling time budget data to list the criteria used for defining time budget categories in each study.

The paucity of sufficiently detailed comparable data for chimpanzees and bonobos restricted the types of questions that could be asked. For example existing feeding and ranging data on chimpanzees do not describe feeding rates and fruit handling times within paths travel rates and distances between patches. Therefore a finer grained analysis of the foraging decisions of chimpanzees cannot be conducted in the same way as analyses on orangutans (e.g. Leighton 1993) and gibbons (e.g. Grether *et al.* 1993). Sex differences and seasonal differences in time budgets could not be examined in detail quantitatively because of the lack of comparative data.

Temperature appears to be a key determinant of baboon time budgets (Dunbar 1992*b*). Similarly, in Japanese macaques (*Macaca fuscata*) (Watanuki & Nakayama 1993) as air temperature decreased animals spent more time resting and less time moving on the ground (although this was partly due to snow cover in cold temperatures). In future models if we are considering conditions of extreme seasonality, we should consider that animals may develop strategies other than time allocation, to balance their

CHAPTER 5. COMPARATIVE PRIMATE SOCIOECOLOGY

CHAPTER 5. COMPARATIVE PRIMATE SOCIOECOLOGY

In this chapter, I first compare the socioecology models developed on extant primate species (gelada baboons, *Papio* baboons, and chimpanzees). I then suggust further model species for models of extant primate socioecology. In the final section (5.3), I extend the models on extant chimpanzees (chapter 4) to make predictions about the maximum ecologically tolerable group size and geographic distribution of the early hominids.

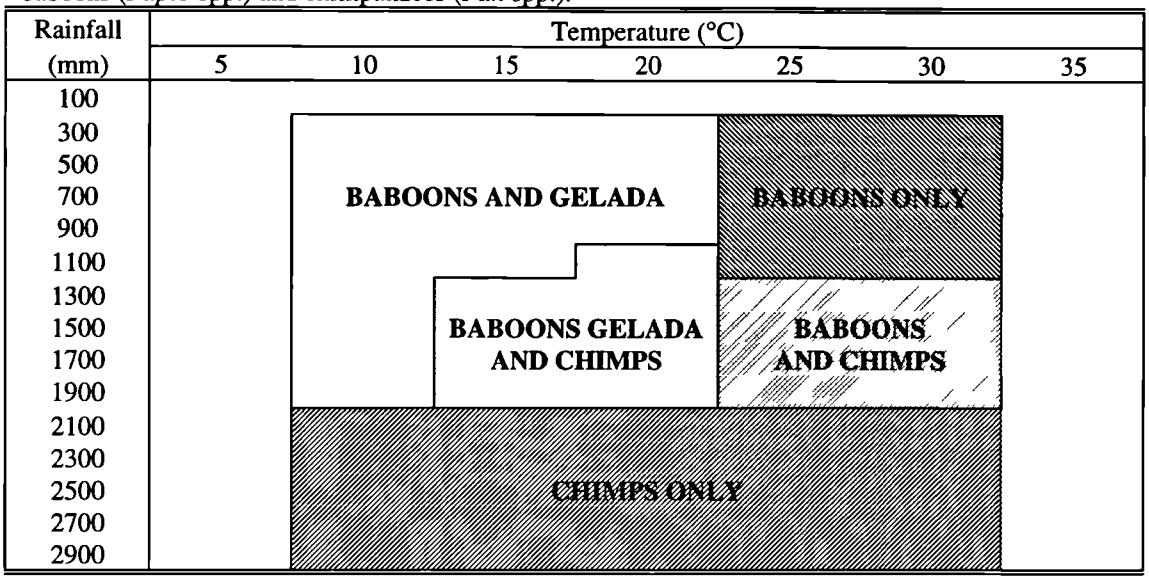
5.1. COMPARISON OF SYSTEMS MODELS OF SOCIOECOLOGY

5.1.1. Comparison of the baboon, gelada and chimpanzee models

With the successful extension of the systems model to the chimpanzees, the results could be compared with those obtained previously on baboons (*Papio* spp.) (chapter 2 this study; Dunbar 1996) and gelada baboons (*Theropithecus gelada*) (Dunbar 1992*a*). Figure 5.1. illustrates graphically the ecologically tolerable zones of the three genera as indicated by their maximum ecologically tolerable group sizes. This figure is similar to that plotted in Dunbar (1996, fig. 5: 47). However, the data presented for the chimpanzee model were preliminary and have subsequently been updated in this study. The 'chimpanzees' referred to in this chapter are the bonobos and chimpanzees modelled together in chapter 4.

The data show that gelada only occur in cooler habitats (10-20°C), consequently the geographic distribution of gelada and *Papio* baboons has a small overlap. In contrast, baboons tend to favour habitats with higher mean temperatures 20-30°. Gelada are restricted in their dietary niche to the grasslands that currently only occur in high altitude habitats (over 1500 meters) (see fig. 2.12.). These only occur in the Simen Highlands of Ethiopia. The distribution of the chimpanzees is a mirror image of that for the baboons, this may reflect dietary differences between the two taxa. Chimpanzees prefer tree-based feeding sites, in contrast to baboons' preference for feeding sites in the shrub / bush layer. The relationship between forest cover and mean annual rainfall (see chapter 4) supports this conclusion.

Figure 5.1. Maximum ecologically tolerable group size of gelada baboons (*Theropithecus gelada*), baboons (*Papio* spp.) and chimpanzees (*Pan* spp.).



The differences between the results of the maximum ecologically tolerable group size models can be seen more graphically in the form of a contour plot (figs 5.2 to 5.4). The first obvious difference between the three models is the straight lines for the gelada results. This was because rainfall did feature in the gelada model (see Dunbar 1992*a*). Gelada maximum ecologically tolerable group sizes were much larger at lower temperatures (around 250) compared to higher temperatures. The contour plots for the baboon maximum ecologically tolerable group sizes show by contrast that the largest maximum group sizes at intermediate rainfalls (1500mm) and highest temperatures. Between 500 and 2000mm rainfall, group sizes remain relatively constant at each temperature integer. However, at very low rainfalls, temperature seems to be most important in constraining group sizes. In wetter habitats, temperature appears to be less of a constraint. For chimpanzees, maximum ecologically tolerable group sizes increase with rainfall, but remain relatively constant across the range of temperatures, except at temperatures above 35°C where groups cannot be sustained due the greatly increased costs of thermoregulation. Rainfall therefore seems to be the primary limiting factor on chimpanzee group sizes. Temperature does not vary significantly between chimpanzee sites (see table 4.9). Rainfall however is a primary determinant of forest cover (see chapter 4), and is therefore important to maintaining habitats suitable for chimpanzees.

Figure 5.2 Chimpanzee maximum ecologically tolerable group size

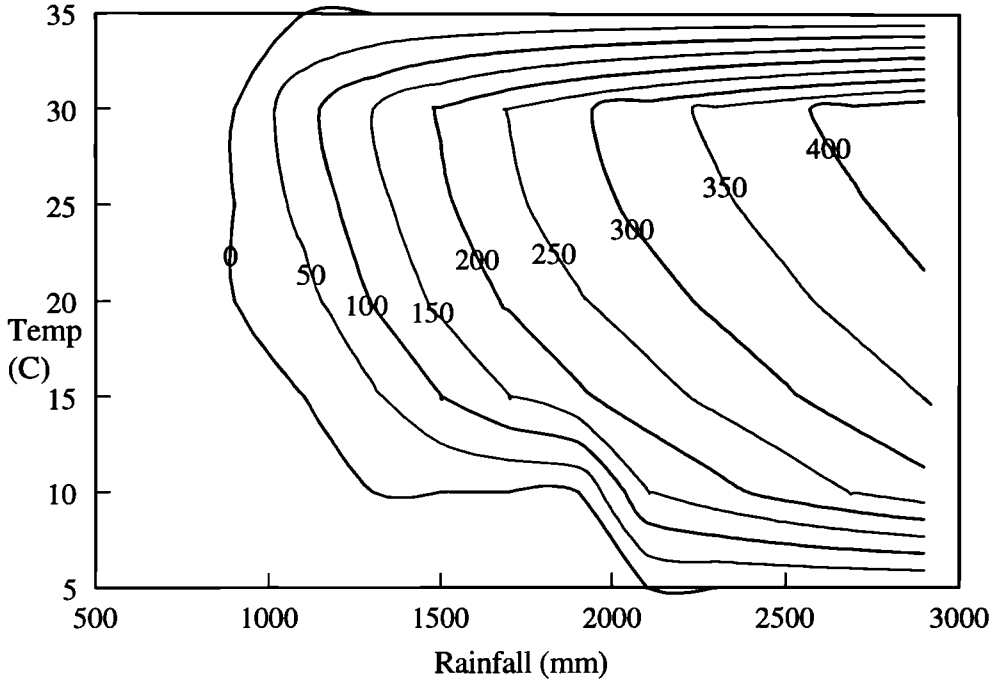


Figure 5.3. Baboon maximum ecologically tolerable group size.

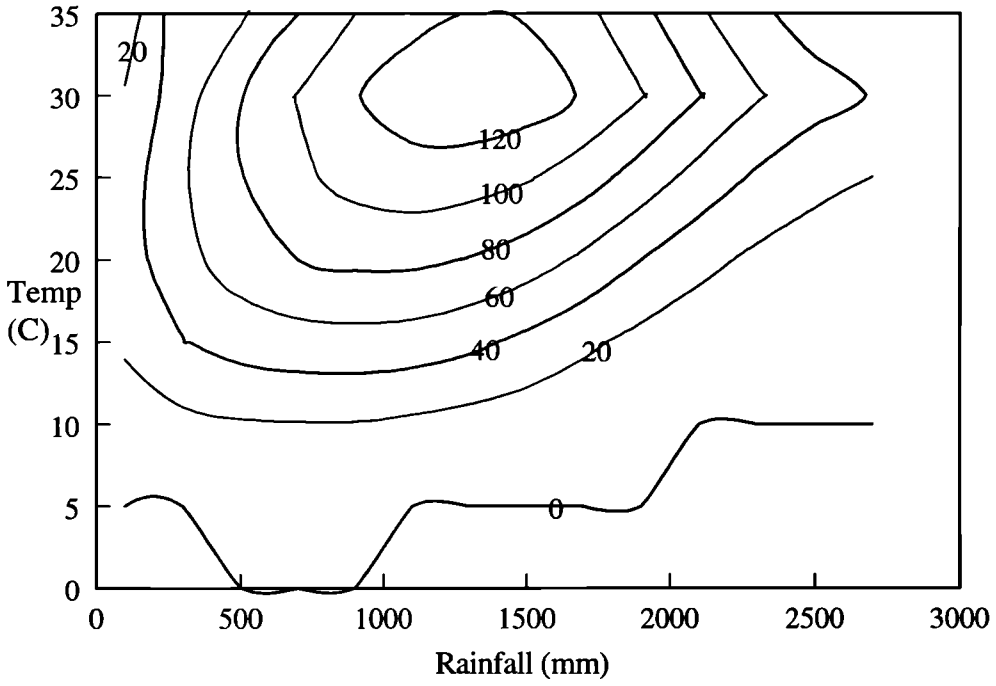
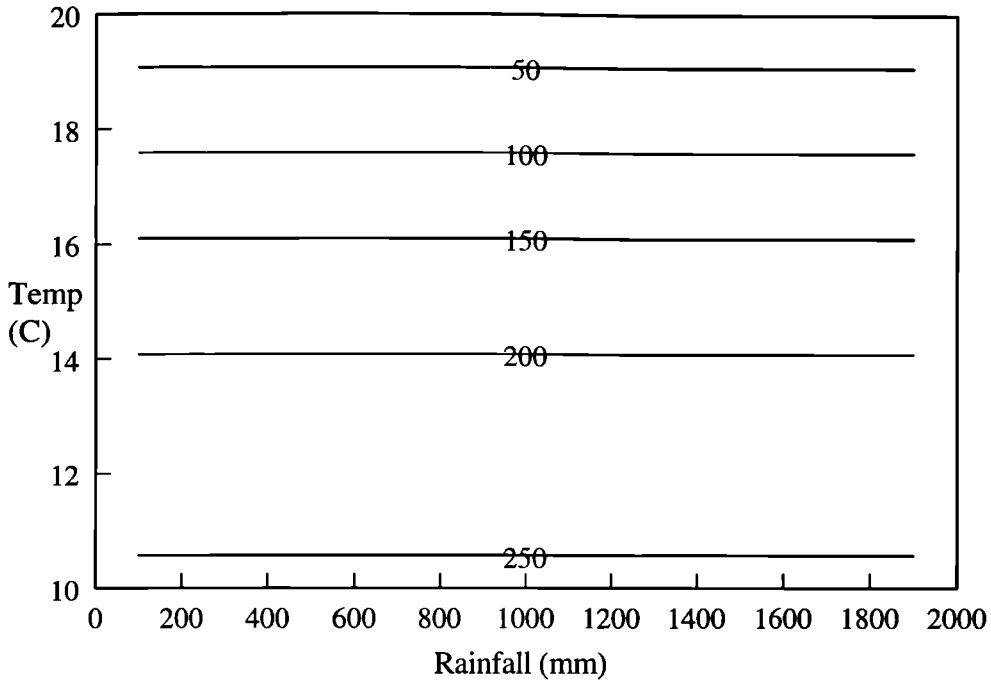


Figure 5.4. Gelada maximum ecologically tolerable group size



The niche separation between the three taxa seems to be the result of dietary differences between them, and the way in which their dietary sources respond to climatic variables. To investigate further the hypothesis that dietary differences separate the three taxa ecologically, the ecological relationships with feeding time can be examined. Table 5.1. gives the time budget equations for each of the three models. The baboon equations are those originally cited in Dunbar (1992*b*), the gelada equations are those published in Dunbar 1992*a*. The chimpanzee equations are those listed in table 4.16 (equation set C).

Table 5.1. Comparison of the equations for gelada (*Theropithecus gelada*) (Dunbar 1992*a*), baboons (*Papio* spp).

Variable	Equation*
Gelada model	
% Feed	$ln\ (F) = 5.94 - 0.60\ ln\ (T) - 0.31\ ln\ (Q)$
% Move	$ln\ (M) = 4.75 + 0.26\ ln\ (J) - 0.49\ ln\ (C)$
% Rest	$R = -12.24 + 2.46\ T$
% Social	$S = 13.26 + 0.02\ N + 0.15\ R$
Day Journey / km	$ln\ (D) = -3.93 + 0.88\ ln\ (N) + 0.85\ ln\ (C)$
Herd Size	$ln\ (J) = 1.25 + 1.08\ ln\ (D) - 1.29\ ln\ (C)$
Baboon model	
% Feed	$ln\ (F) = 6.37 - 0.66\ ln\ (T) + 5.65\ ln\ (Z)$
	$ln\ (F) = 7.41 - 0.88\ ln\ (T) + 4.44\ ln\ (Z) - 0.45\ ln\ (Mo50) + 0.16\ ln\ (D)$
% Move	$ln\ (M) = 2.20 + 0.16\ ln\ (N) + 0.22\ ln\ (Mo50)$
% Rest	$ln\ (R) = 10.55 - 1.33\ ln\ (F) - 0.22\ ln\ (N) - 0.98\ ln\ (P)$
% Social	$ln\ (S) = -1.60 + 0.49\ ln\ (P) - 4.97\ ln\ (Z)$
Day Journey / km	$ln\ (D) = 1.34 + 0.78\ ln\ (N) - 0.47\ ln\ (P)$
Chimpanzee model	
% Feed	$\ln(F) = 4.8850 - 0.6744\ \ln(PARTY) - 0.081\ln(DEN)$
% Rest + social	$\ln(R/S) = 0.9092 + 0.3589\ \ln(P) + 0.045\ \ln(DEN)$
% Move	$\ln(M) = 2.9054 + 0.026\ \ln(Mo50) - 0.049\ \ln(T) + 0.0458\ \ln(DEN)$
Day Journey / km	$\ln(D) = 2.8792 - 0.6349\ \ln(HR)$
Party size	$\ln(PARTY) = -0.6106 + 1.082\ \ln(P) - 0.0625\ \ln(N)$
	or, $\ln(PARTY) = -8.1356 + 1.3229\ \ln(P) - 0.0748\ \ln(DEN)$
Density (animals /km^2)	$\ln(DEN) = -18.925 + 0.2624\ \ln(N) + 2.5338\ \ln(P)$
Community size	$\ln(N) = 4.4510 + 0.0927\ \ln(T) + 5.22\ \ln(Z)$
Home range area (km^2)	$\ln(HR) = 3.6301 - 0.8326\ \ln(DEN) - 0.094\ \ln(Mo50)$

* F = % feeding time; M = % moving time; R = % resting time; S = % social time; R/S = % resting + social time (chimpanzees only); D = day journey length (km); N = group size; Q = protein content in grasses (% protein by weight); C = % grass cover; Z = Simpson's index of rainfall diversity; Mo50 = number of months with <50mm rainfall; P = mean annual rainfall; PARTY = mean party size; DEN = density (animals / km^2); HR = home range area (km^2).

The feeding time equation in the gelada model has temperature and the protein content of grasses as predictors. The baboon feeding time equation has temperature and rainfall seasonality as predictors. The protein content of grasses is related positively to

temperature, $\ln(Q) = -26.7 + 23.9 \ln(T) - 4.8(\ln(T))^2$ ($r^2 = 0.97$) as is Simpson's index of rainfall diversity $\ln(Z) = -4.9 + 3.2 \ln(T) - 0.6(\ln(T))^2$ ($r^2 = 0.65$) (Dunbar 1996). In habitats where baboons have a high feeding time, gelada have to feed relatively little, and vice versa. This is a consequence of the opposite responses of grass and bush density to temperature. The grasses upon which gelada feed are common at low temperatures, whereas the bush level vegetation baboons require are common at relatively higher temperatures. Time spent moving in baboons and gelada reflects these dietary differences, since time spent moving is assumed to be negatively related to vegetation density.

By contrast to the gelada and baboon models, ecological variables do not enter the feeding time equation directly. This is partly a consequence of the small sample sizes used in the analysis, and the uneven distribution of habitat types in the time budget data set (e.g. paucity of 'savanna' chimpanzee site data). Party size and density, enter the equation for feeding time, and the prime determinant of each of these variables is mean annual rainfall. Rainfall was shown to correlate highly with forest cover (chapter 4), therefore by inference the amount of time chimpanzees spend feeding is related to the degree of forest cover.

Although rainfall was identified as the primary factor regulating food availability for chimpanzees, this is not universal for all forest living primates. For example, rainfall does directly affect vervet female feeding activities, which could be the result of guenon foods being still abundant in the first part of the dry season (Butynski 1988). Similarly the lack of significant equations for the gibbons (Sear 1994), could be due to the fact that their arboreal diet does not respond as quickly to rainfall as grasses.

5.1.2. Discussion

To conclude, the difference between the chimpanzee, baboon and gelada maximum ecologically tolerable group sizes can be separated on dietary grounds. If the model socioecology based on time-budgets is to be transferable across species, dietary factors need to be taken into account. This is particularly important with regard to the minimum

time allocation for resting needed for digestion. Where foods contain high levels of fibre, animals allocate more time for resting (e.g. ungulates: Jenks & Leslie 1989; Illius & Gordon 1990). The digestive organ passage time could constraint the bulk intake of diet per day in primates.

Seasonality emerged as an important variable in the chimpanzee and baboon time budget equations. There are essentially two strategies for animals in periods of food shortage in highly seasonal environments; to increase foraging effort or to increase inactive time to conserve energy (e.g. Gederlund *et al.* 1989). Gorillas are confined to regions with no more than four dry months per year (if a dry month <100mm), whereas chimpanzees can tolerate up to five dry months per year. By contrast *Australopithecus afarensis* has been discovered in areas that at present have more than five dry months per year. These hominid habitats are likely to have been similarly dry in the past (Aronson & Taieb 1981). Chimpanzees range more widely in savannas (Suzuki 1969; Kano 1972; Baldwin *et al.*, 1982). Given these assumptions, and that hominids had comparable diet to chimpanzees, a savanna hominid would have to travel further, and have longer day journey lengths than a forest hominid (Moore 1996).

5.2. OTHER EXTANT SPECIES FOR SOCIOECOLOGICAL MODELS.

Other candidates for socioecological modelling could have been considered for example mountain gorillas (*Gorilla gorilla*), however there were insufficient time budget data for detailed analysis. The earliest data available on mountain gorilla time budgets (Fossey & Harcourt 1977) is considered anomalous since the influence of body size on time spent feeding was found to be opposite to that from studies of other primate species (Watts 1988). A re-study (Harcourt & Stewart 1984) removed the methodological artefact at fault in the earlier study. There are however, very few studies on mountain gorilla time budgets, Watts (1988) provides the only data. Watts (1988) found that the majority of gorilla daily activity budgets were spent feeding, the majority of the remaining time, spent resting. A minority of overall time was spent moving or socialising. Significant variation was found in activity budgets between different vegetation zones used by the

gorillas. Time spent feeding was found to be directly proportional to group size. However the effect of group size on feeding time was less than that of food quality and distribution.

Table 5.2. Mean time budgets for mountain gorillas (data from Watts 1988).

Time budget (%)*				
Feed	Move	Rest	Social	Other
59.67	30.27	6.89	2.87	0.34

* Data from Watts (1988, group 4 only, table II: 200). Data are means of seven habitat zones, and therefore sum to greater than 100%.

Day journey length data for gorillas were more widely available than time budget data (e.g. Yamagiwa 1986; Yamagiwa & Mwanda 1994). Solitary males in the tropical forest of Zaire have longer day journey lengths, visit more types of vegetation and consume a more varied diet. By contrast, males in the Virunga Mountains have a larger number of feeding sites per day and a greater mean distance between foraging sites (Yamagiwa & Mwanda 1994). Habitat differences between the highland Virungas and the lowland Zaire habitats accounted for the difference in day journey lengths.

Whilst there were insufficient data on gorillas to conduct a comparative analysis, their use as a conceptual model may be question on several grounds. Gorillas, whilst being large bodied terrestrial primates, have very specialised dietary adaptations. Therefore in extending the model to an extint taxa, compensation would need to be taken of this fact.

CHAPTER 5. COMPARATIVE PRIMATE SOCIOECOLOGY

In this chapter, I first compare the socioecology models developed on extant primate species (gelada baboons, *Papio* baboons, and chimpanzees). I then suggust further model species for models of extant primate socioecology. In the final section (5.3), I extend the models on extant chimpanzees (chapter 4) to make predictions about the maximum ecologically tolerable group size and geographic distribution of the early hominids.

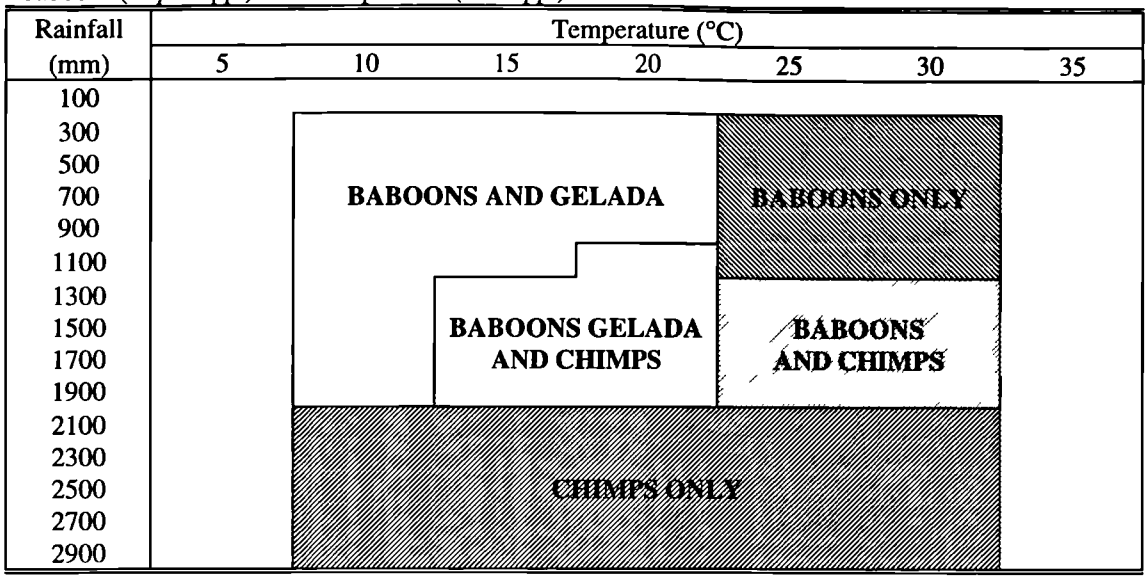
5.1. COMPARISON OF SYSTEMS MODELS OF SOCIOECOLOGY

5.1.1. Comparison of the baboon, gelada and chimpanzee models

With the successful extension of the systems model to the chimpanzees, the results could be compared with those obtained previously on baboons (*Papio* spp.) (chapter 2 this study; Dunbar 1996) and gelada baboons (*Theropithecus gelada*) (Dunbar 1992*a*). Figure 5.1. illustrates graphically the ecologically tolerable zones of the three genera as indicated by their maximum ecologically tolerable group sizes. This figure is similar to that plotted in Dunbar (1996, fig. 5: 47). However, the data presented for the chimpanzee model were preliminary and have subsequently been updated in this study. The 'chimpanzees' referred to in this chapter are the bonobos and chimpanzees modelled together in chapter 4.

The data show that gelada only occur in cooler habitats (10-20°C), consequently the geographic distribution of gelada and *Papio* baboons has a small overlap. In contrast, baboons tend to favour habitats with higher mean temperatures 20-30°. Gelada are restricted in their dietary niche to the grasslands that currently only occur in high altitude habitats (over 1500 meters) (see fig. 2.12.). These only occur in the Simen Highlands of Ethiopia. The distribution of the chimpanzees is a mirror image of that for the baboons, this may reflect dietary differences between the two taxa. Chimpanzees prefer tree-based feeding sites, in contrast to baboons' preference for feeding sites in the shrub / bush layer. The relationship between forest cover and mean annual rainfall (see chapter 4) supports this conclusion.

Figure 5.1. Maximum ecologically tolerable group size of gelada baboons (*Theropithecus gelada*), baboons (*Papio* spp.) and chimpanzees (*Pan* spp.).



The differences between the results of the maximum ecologically tolerable group size models can be seen more graphically in the form of a contour plot (figs 5.2 to 5.4). The first obvious difference between the three models is the straight lines for the gelada results. This was because rainfall did feature in the gelada model (see Dunbar 1992*a*). Gelada maximum ecologically tolerable group sizes were much larger at lower temperatures (around 250) compared to higher temperatures. The contour plots for the baboon maximum ecologically tolerable group sizes show by contrast that the largest maximum group sizes at intermediate rainfalls (1500mm) and highest temperatures. Between 500 and 2000mm rainfall, group sizes remain relatively constant at each temperature integer. However, at very low rainfalls, temperature seems to be most important in constraining group sizes. In wetter habitats, temperature appears to be less of a constraint. For chimpanzees, maximum ecologically tolerable group sizes increase with rainfall, but remain relatively constant across the range of temperatures, except at temperatures above 35°C where groups cannot be sustained due the greatly increased costs of thermoregulation. Rainfall therefore seems to be the primary limiting factor on chimpanzee group sizes. Temperature does not vary significantly between chimpanzee sites (see table 4.9). Rainfall however is a primary determinant of forest cover (see chapter 4), and is therefore important to maintaining habitats suitable for chimpanzees.

Figure 5.1. & 5.2 (contour plot)

Figure 5.3 (contour plot)

The niche separation between the three taxa seems to be the result of dietary differences between them, and the way in which their dietary sources respond to climatic variables. To investigate further the hypothesis that dietary differences separate the three taxa ecologically, the ecological relationships with feeding time can be examined. Table 5.1. gives the time budget equations for each of the three models. The baboon equations are those originally cited in Dunbar (1992*b*), the gelada equations are those published in Dunbar 1992*a*. The chimpanzee equations are those listed in table 4.16 (equation set C).

Table 5.1. Comparison of the equations for gelada (*Theropithecus gelada*) (Dunbar 1992*a*), baboons (*Papio* spp).

Variable	Equation*
Gelada model	
% Feed	$ln\ (F) = 5.94 - 0.60\ ln\ (T) - 0.31\ ln\ (Q)$
% Move	$ln\ (M) = 4.75 + 0.26\ ln\ (J) - 0.49\ ln\ (C)$
% Rest	$R = -12.24 + 2.46\ T$
% Social	$S = 13.26 + 0.02\ N + 0.15\ R$
Day Journey / km	$ln\ (D) = -3.93 + 0.88\ ln\ (N) + 0.85\ ln\ (C)$
Herd Size	$ln\ (J) = 1.25 + 1.08\ ln\ (D) - 1.29\ ln\ (C)$
Baboon model	
% Feed	$ln\ (F) = 6.37 - 0.66\ ln\ (T) + 5.65\ ln\ (Z)$ $ln\ (F) = 7.41 - 0.88\ ln\ (T) + 4.44\ ln\ (Z) - 0.45\ ln\ (Mo50) + 0.16\ ln\ (D)$
% Move	$ln\ (M) = 2.20 + 0.16\ ln\ (N) + 0.22\ ln\ (Mo50)$
% Rest	$ln\ (R) = 10.55 - 1.33\ ln\ (F) - 0.22\ ln\ (N) - 0.98\ ln\ (P)$
% Social	$ln\ (S) = -1.60 + 0.49\ ln\ (P) - 4.97\ ln\ (Z)$
Day Journey / km	$ln\ (D) = 1.34 + 0.78\ ln\ (N) - 0.47\ ln\ (P)$
Chimpanzee model	
% Feed	$\ln(F) = 4.8850 - 0.6744\ \ln(PARTY) - 0.081\ln(DEN)$
% Rest + social	$\ln(R/S) = 0.9092 + 0.3589\ \ln(P) + 0.045\ \ln(DEN)$
% Move	$\ln(M) = 2.9054 + 0.026\ \ln(Mo50) - 0.049\ \ln(T) + 0.0458\ \ln(DEN)$
Day Journey / km	$\ln(D) = 2.8792 - 0.6349\ \ln(HR)$
Party size	$\ln(PARTY) = -0.6106 + 1.082\ \ln(P) - 0.0625\ \ln(N)$ or, $\ln(PARTY) = -8.1356 + 1.3229\ \ln(P) - 0.0748\ \ln(DEN)$
Density (animals /km^2)	$\ln(DEN) = -18.925 + 0.2624\ \ln(N) + 2.5338\ \ln(P)$
Community size	$\ln(N) = 4.4510 + 0.0927\ \ln(T) + 5.22\ \ln(Z)$
Home range area (km^2)	$\ln(HR) = 3.6301 - 0.8326\ \ln(DEN) - 0.094\ \ln(Mo50)$

* F = % feeding time; M = % moving time; R = % resting time; S = % social time; R/S = % resting + social time (chimpanzees only); D = day journey length (km); N = group size; Q = protein content in grasses (% protein by weight); C = % grass cover; Z = Simpson's index of rainfall diversity; Mo50 = number of months with <50mm rainfall; P = mean annual rainfall; PARTY = mean party size; DEN = density (animals / km^2); HR = home range area (km^2).

The feeding time equation in the gelada model has temperature and the protein content of grasses as predictors. The baboon feeding time equation has temperature and rainfall seasonality as predictors. The protein content of grasses is related positively to

temperature, $\ln(Q) = -26.7 + 23.9 \ln(T) - 4.8(\ln(T))^2$ ($r^2 = 0.97$) as is Simpson's index of rainfall diversity $\ln(Z) = -4.9 + 3.2 \ln(T) - 0.6(\ln(T))^2$ ($r^2 = 0.65$) (Dunbar 1996). In habitats where baboons have a high feeding time, gelada have to feed relatively little, and vice versa. This is a consequence of the opposite responses of grass and bush density to temperature. The grasses upon which gelada feed are common at low temperatures, whereas the bush level vegetation baboons require are common at relatively higher temperatures. Time spent moving in baboons and gelada reflects these dietary differences, since time spent moving is assumed to be negatively related to vegetation density.

By contrast to the gelada and baboon models, ecological variables do not enter the feeding time equation directly. This is partly a consequence of the small sample sizes used in the analysis, and the uneven distribution of habitat types in the time budget data set (e.g. paucity of 'savanna' chimpanzee site data). Party size and density, enter the equation for feeding time, and the prime determinant of each of these variables is mean annual rainfall. Rainfall was shown to correlate highly with forest cover (chapter 4), therefore by inference the amount of time chimpanzees spend feeding is related to the degree of forest cover.

Although rainfall was identified as the primary factor regulating food availability for chimpanzees, this is not universal for all forest living primates. For example, rainfall does directly affect vervet female feeding activities, which could be the result of guenon foods being still abundant in the first part of the dry season (Butynski 1988). Similarly the lack of significant equations for the gibbons (Sear 1994), could be due to the fact that their arboreal diet does not respond as quickly to rainfall as grasses.

5.1.2. Discussion

To conclude, the difference between the chimpanzee, baboon and gelada maximum ecologically tolerable group sizes can be separated on dietary grounds. If the model socioecology based on time-budgets is to be transferable across species, dietary factors need to be taken into account. This is particularly important with regard to the minimum

time allocation for resting needed for digestion. Where foods contain high levels of fibre, animals allocate more time for resting (e.g. ungulates: Jenks & Leslie 1989; Illius & Gordon 1990). The digestive organ passage time could constraint the bulk intake of diet per day in primates.

Seasonality emerged as an important variable in the chimpanzee and baboon time budget equations. There are essentially two strategies for animals in periods of food shortage in highly seasonal environments; to increase foraging effort or to increase inactive time to conserve energy (e.g. Gederlund *et al.* 1989). Gorillas are confined to regions with no more than four dry months per year (if a dry month <100mm), whereas chimpanzees can tolerate up to five dry months per year. By contrast *Australopithecus afarensis* has been discovered in areas that at present have more than five dry months per year. These hominid habitats are likely to have been similarly dry in the past (Aronson & Taieb 1981). Chimpanzees range more widely in savannas (Suzuki 1969; Kano 1972; Baldwin *et al.*, 1982). Given these assumptions, and that hominids had comparable diet to chimpanzees, a savanna hominid would have to travel further, and have longer day journey lengths than a forest hominid (Moore 1996).

5.2. OTHER EXTANT SPECIES FOR SOCIOECOLOGICAL MODELS.

Other candidates for socioecological modelling could have been considered for example mountain gorillas (*Gorilla gorilla*), however there were insufficient time budget data for detailed analysis. The earliest data available on mountain gorilla time budgets (Fossey & Harcourt 1977) is considered anomalous since the influence of body size on time spent feeding was found to be opposite to that from studies of other primate species (Watts 1988). A re-study (Harcourt & Stewart 1984) removed the methodological artefact at fault in the earlier study. There are however, very few studies on mountain gorilla time budgets, Watts (1988) provides the only data. Watts (1988) found that the majority of gorilla daily activity budgets were spent feeding, the majority of the remaining time, spent resting. A minority of overall time was spent moving or socialising. Significant variation was found in activity budgets between different vegetation zones used by the

gorillas. Time spent feeding was found to be directly proportional to group size. However the effect of group size on feeding time was less than that of food quality and distribution.

Table 5.2. Mean time budgets for mountain gorillas (data from Watts 1988).

Time budget (%)*				
Feed	Move	Rest	Social	Other
59.67	30.27	6.89	2.87	0.34

* Data from Watts (1988, group 4 only, table II: 200). Data are means of seven habitat zones, and therefore sum to greater than 100%.

Day journey length data for gorillas were more widely available than time budget data (e.g. Yamagiwa 1986; Yamagiwa & Mwanda 1994). Solitary males in the tropical forest of Zaire have longer day journey lengths, visit more types of vegetation and consume a more varied diet. By contrast, males in the Virunga Mountains have a larger number of feeding sites per day and a greater mean distance between foraging sites (Yamagiwa & Mwanda 1994). Habitat differences between the highland Virungas and the lowland Zaire habitats accounted for the difference in day journey lengths.

Whilst there were insufficient data on gorillas to conduct a comparative analysis, their use as a conceptual model may be question on several grounds. Gorillas, whilst being large bodied terrestrial primates, have very specialised dietary adaptations. Therefore in extending the model to an extint taxa, compensation would need to be taken of this fact.

5.3. A CONCEPTUAL MODEL FOR THE EARLY HOMINIDS

5.3.1. Introduction

The behavioural ecological perspective for reconstructing the behaviour of the early hominids relies on the theory of ecological uniformitarianism (see Gifford-Gonzalez 1991). The models developed in this study appear to work extremely well for members of the extant genera for which they apply. The valid extension of the model to the extinct hominids depends on three key assumptions:

1. Fairly precise body weights for extinct animals are established
2. Values for simple climatic variables, such as rainfall and temperature need to be defined for palaeohabitats. The finding that a very small number of environmental variables are needed to characterise habitats (chapter 2) is useful in this context.
3. The assumption is that the extinct taxa should be ecologically similar to the extant taxa on which the model is based.

To extrapolate the chimpanzee model to the australopithecines, the same ecological principles and processes that underlie the basic structure of plant communities today, are assumed to have operated in the past (Behrensmeyer 1982; Bell 1982; Foley 1984; Sept 1992). The Plio-Pleistocene vegetation mosaic appears to have been broadly similar to the present day landscape (e.g. Bonnefille 1984; Bonnefille & Vincens 1985), and the fossil record suggests modern faunal relationships have relevance for past interactions (e.g. Blumenschine 1986; Marean 1989; Blumenschine *et al.* 1994). Controversy still remains over the detailed environmental setting of the australopithecines. Evidence from most sites suggests some form of vegetation mosaic, comprising dense vegetation (including sub-tropical forest), and relatively open bush (e.g. Avery 1995; Rayner *et al.* 1993; Kingston *et al.* 1994), although a more consistently wooded habitat has been suggested for some sites (Cerling 1992; Kingston *et al.* 1994). The location of all australopithecine sites in heterogenous environments supports the suggestion that hominids adopted a generalist strategy (Avery 1995). Associated faunas suggest that

Ardipithecus lived in well wooded habitats (White *et al.* 1994, 1995; Woldegabriel *et al.* 1994).

In addition to palaeoenvironmental data, studies of plant food availability have been conducted in a range of environments in eastern and southern Africa (e.g. Peters & Maguire 1981; Peters *et al.* 1984; O'Brien & Peters 1991; Sept 1994). These studies build up effective "frames of reference" for the interpretation of archaeological sites. Whilst care must be taken not to attribute features of a contemporary ecosystem to a prehistoric one, on the basis of a few similiarities ("transferred ecology", or "neo-ecology": Lawrence 1971; Blumenschine *et al.* 1994), the probable general ecological uniformitarianism of post-Miocene savanna and mosaic environments allows detailed studies of modern settings to be applied to the understanding of ancient habitats. Studies of the physical environment and the distribution of resources within these habitats, such as those recorded around Makapansgat, South Africa (Williamson, unpublished data), provide information of fundamental importance to palaeoecological models.

Dental studies suggest that australopithecine and chimpanzee diets were broadly similar (e.g. Grine & Kay 1988; Andrews & Martin 1991). Australopithecines may have been primarily vegetarian (Walker 1981), largely frugivorous (*A. afarensis*: Andrews & Martin 1992), or had a seasonal reliance on gritty foods (Peters 1987; Ryan & Johanson 1989). Thackeray (*pers comm.* 1996) has suggested, however, that australopithecines may have been omnivorous, scavenging when carcasses were available.

In this section I present simple modifications to the chimpanzee socioecology model to extend their predictions to the early hominids. The models have proved flexible enough to be extended from the baboons to the chimpanzees; the final step in this study is to extend them to the early hominids.

5.3.2. Adjusting the chimpanzee model

The chimpanzee model is thought an appropriate model species for extending to the early hominids on several grounds. Firstly on phylogenetic grounds, in the shared ancestry of the early hominids and chimpanzees, secondly on ecological grounds, where the early hominids, like the chimpanzees, were thought to have occupied open woodland. The divergence between human ancestors and chimpanzees is thought to have occurred around 7 to 5mya. The behaviours exhibited by the early hominids are assumed to have been within the range of variability of the extant chimpanzees (Foley 1996).

Adjust equations for body weight

In order to extend the analyses on extant primates to extinct species it is necessary to take body weight into account. The analyses on chimpanzees assumed that body weight was constant across chimpanzee populations. The values for feeding and moving time predicted by the equations can be corrected using the following scalars (see Dunbar 1992*e*):

$$F_w = F \times W^{0.404}/B^{0.404}$$

$$M_w = M \times B^{0.303}/W^{0.303}$$

Where F is the percentage of time spent feeding, M the time spent moving, W the mean adult body weight of the target population and B the mean adult body weight for the sample of populations from which the equations were derived. The scalar for feeding time takes both the metabolic costs of thermoregulation and the increased efficiency of digestion into account (Demment & van Soest 1985). The scalar for moving time compensates for the increased stride length of larger animals (Peters 1983). Table 5..3. gives estimates of body weight for the extinct taxa, and details of the sites from which they are found. There have been a number approaches to predict the body weight of the extinct hominids using both post-cranial and cranial measurements (e.g. post-cranial measurements: e.g. Hartwig-Scherer 1993; McHenry 1992, 1994; cranial measurements:

Aiello & Wood 1994). The body weights taken for the analyses presented here are those published in McHenry (1994), which take linear dimensions from the axial skeleton and from the shafts and articular surfaces of long bones. The assumptions of these measurements is that the post-cranial skeletal dimensions are more tightly constrained by body mass.

Table 5.3. Body weight and habitat variables for the australopithecines.

Species	Fossil site location	Geological age (mya)	Estimated male weight (kg)	Estimated female weight (kg)	Mean species weight (kg)
A. anamensis	Kanapoi (Kenya)	3.9 - 4.2			58.0**
A. afarensis	Hadar (Ethiopia) Middle Awash (Ethiopia) Laetoli (Tanzania)	4.0 - 2.9	44.6±18.5	29.3±15.7	37.0±17.1
A. africanus	Taung (S. Afr) Sterkfontein (S. Afr) Swartkrans (S. Afr) Makapansgat (S. Afr)	3.0 - 2.4	40.8±17.3	30.2±19.5	35.5±18.4
P. robustus	Swartkrans (S. Afr) Kroodraai (S. Afr)	1.8 - 1.6	40.2±15.8	31.9±21.5	36.1±18.7
P. boisei	Omo (Ethiopia) E. Turkana (Kenya) W. Turkana (Kenya) Chesowanja Peninj Olduvai Gorge	2.0 - 1.3	48.6±34.6	34.0±13.7	44.3±24.2

* Body weight estimates from McHenry 1996. ** Estimated in Leakey *et al.* (1995) based on the regression equations in McHenry 1992.

5.3.3. Model inputs

In the extension of the extant Papio model (Dunbar 1992*a*) to the extinct Papionines (Dunbar 1992*e*) the climatic parameters used were those given in Carr (1976), Bonnefille (1983), Shipman & Harris (1988) and Vrba (1988). Shipman & Harris (1988) provide estimates of temperature and rainfall for some key Papionine fossil sites, by matching fossil faunal distributions at these sites to the extant faunas for a number of African habitats. The current climate for the area that has the most similar faunal profile is taken as the best estimate of the palaeo-climate at a given horizon, on the assumption that habitats characterised by similar faunal (particularly ungulate) profiles are likely to have similar vegetational conditions. Reconstructions of palaeocecology have in the past

concentrated on species organization and the composition of the fossil fauna recovered from a particular locality (Dodd & Stanton 1990). Mean ambient temperature for a given contemporary habitat can be determined from its altitude and latitude using the equation predicting temperature from altitude and latitude (Dunbar 1992e)

$$T = 28.36 - 0.0048A - 0.18L$$

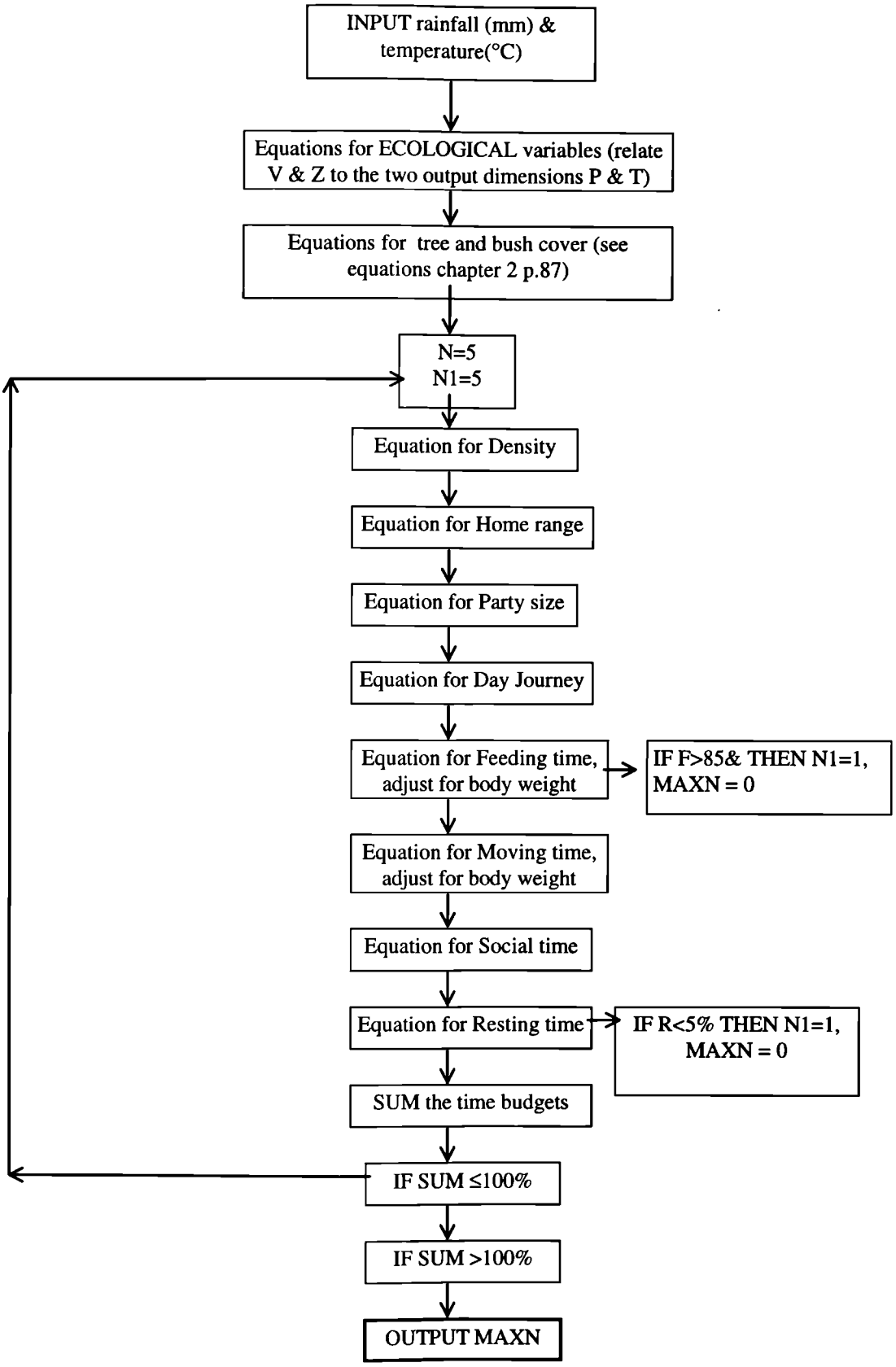
where, T = mean annual temperature (°C), A = altitude and L = latitude. The habitats occupied by the australopithecines was fairly static (Stanley 1992; Reed 1997), and the australopithecines could have existed in habitats constrained by a minimum and maximum amount of rainfall and tree cover. Over time, mammalian communities indicate that habitats became more open and the australopithecines disappear from the fossil record. Reed (1997) suggests that a gradual change to drier more open habitats and a more pronounced dry season forced the australopithecines across an environmental tolerance limit around 2.8 to 2.5 mya and resulted in their extinction.

Construction of the BASIC *model*

The model prediction chimpanzee maximum ecologically tolerable group size (N_{max}) (see appendix III, part 3 for the program written in BASIC) was modified in several ways. This model predicted N_{max} for known environmental inputs (rainfall and temperature), and the chimpanzee time budgets were scaled for australopithecine body size (see above). The flow diagram in figure 5.5 illustrates the features of the revised N_{max} prediction program. For known inputs of rainfall and temperature, the model can predict a maximum ecologically tolerable group size.

In addition to the revised BASIC model, the original chimpanzee model was used, using the equations derived for the chimpanzee socioecology model (table 4.16.c. p.180) but with the feeding and moving time equations adjusted for differences in body weight between the chimpanzees and australopithecines (see above). In contrast to the revised model which predicts N_{max} for specific rainfall and temperature values, the original model predicts N_{max} for integers of rainfall and temperature.

Figure 5.5. Flow diagram illustrating the revised N_{max} prediction program for the australopithecines.



Key: MAXN = maximum ecologically tolerable group size; N = group size.

5.3.4. Results

Chimpanzee socioecology model adjusted for australopithecine body weight

The original chimpanzee socioecology model was run, adjusting for the different body weights of the gracile and robust australopithecines (see table 5.3), the results are presented in tables 5.4.a to e. As body weight increases the model predicts that the early hominids are less able to inhabit colder habitats (<15°C), and cannot sustain groups in habitats with rainfall <1100mm (table 5.4.c).

To investigate the effect of a range of body weights on the habitats the chimpanzee socioecology model predicted species could sustain groups in, a range of body weights (30-90kg) were used as inputs. Table 5.5. illustrates the range of rainfall values at integers of temperature (0 to 35°C) that species of a range of body weights could occupy. Species of smaller body weight could exist in colder and drier climates. Above 50kg body weight, the chimpanzee time budget model predicted that species could not inhabit areas with temperatures <15°C. The large body size of *A. anamensis* may be not be representative of the species, but given the paucity of fosil evidence is the best estimate of body weight available at present. The examination of a range of body weights in the chimpanzee model allows us to make predictions given the available fossil evidence.

Predicting maximum australopithecine group size in extant chimpanzee habitats.

For each species of australopithecine, maximum ecologically tolerable group size was predicted for the known rainfall and temperature values for extant chimpanzee habitats (see table 4.9, p. 162 for sources for chimpanzee climate data). The habitat type for each chimpanzee habitat has been well characterised (see chapter 4), and therefore serves as a good test of the types of habitats australopithecines may have inhabited. There is very little qualitative difference between the species in the chimpanzee habitats in which they could sustain groups. The larger *A. anamensis* was predicted not to have existed in the hot, dry west African habitat of Assirik. The largest group sizes for the

australopithecines occur in the wetter forested areas, currently in the Zaire basin (bonobo habitats).

Australopithecine N_{max} group size in a range of habitat types

The effect of body weight on habitat 'preference', as predicted by the chimpanzee socioecology model, values for N_{max} were predicted for each species in three habitat types: savanna, open woodland and closed forest. The equations in table 2.13 (chapter 2, p. 75), were used to help define these three habitat types. As discussed in chapter 2, the number of dry months (a dry month is defined as having <50mm rainfall) is critical in characterising the vegetation structure of habitats, in both the Old and New World. Habitats with between 0 and 3 dry months were classified as forest, 4 to 8 months as woodland and 9 to 12 months as savanna. The mean annual rainfall associated with each of these thresholds of dry months is listed in table 2.13. Using the African rainfall compilation compiled from Wernstedt (1972) (n=218 weather stations), 15 weather stations were randomly sampled from each habitat type. Where temperature was unavailable, the equation relating alitude and latitude (see above) was used to predict mean annual temperature. These rainfall and temperature values were then used as inputs for the revised chimpanzee maximum ecologically tolerable group size model. The results of these three simulations are listed in figures 5.7.a to c.

None of the 6 focus species were predicted by the model to be able to sustain groups in the savanna habitats, as defined here. Groups could be sustained in both woodland and forest habitats. The mean N_{max} for each species in each habitat is illustrated in figure 5.6, larger group sizes were sustained by all species in the forest habitat compared to the open woodland habitats.

The consequences for species distributions after the disruption of the east African habitat due to rifting is illustrated in figure 5.7. One consequence of rifting is the breaking up of habitat types, which has consequences for species distributions, speciation and extinction events. The model presented here predicts that all the robust and gracile australopithecines occupied both forest and woodland habitats, but not savanna habitats.

Table 5.4.a. Maximum ecologically tolerable group size: *Australopithecus afarensis*.

Rain	Temperature (°C)							
(mm)	**0**	**5**	**10**	**15**	**20**	**25**	**30**	**35**
100	0	0	0	0	0	0	0	0
300	0	0	0	0	0	0	0	0
500	0	0	0	0	0	0	0	0
700	0	0	0	0	0	0	0	0
900	0	0	0	0	0	0	0	0
1100	0	0	0	0	33	67	86	0
1300	0	0	0	42	104	135	151	0
1500	0	0	0	101	161	192	206	0
1700	0	0	0	150	207	239	252	0
1900	0	0	0	192	245	280	293	0
2100	0	0	149	229	279	314	329	0
2300	0	0	186	263	310	342	361	0
2500	0	0	221	294	338	369	391	0
2700	0	0	253	324	366	395	416	0
2900	0	0	283	350	391	418	439	0

Table 5.4.b. Maximum ecologically tolerable group size: *Australopithecus africanus*.

Rain	Temperature (°C)							
(mm)	**0**	**5**	**10**	**15**	**20**	**25**	**30**	**35**
100	0	0	0	0	0	0	0	0
300	0	0	0	0	0	0	0	0
500	0	0	0	0	0	0	0	0
700	0	0	0	0	0	0	0	0
900	0	0	0	0	0	0	0	0
1100	0	0	0	0	33	67	59	0
1300	0	0	0	42	104	135	151	0
1500	0	0	0	101	161	192	206	0
1700	0	0	0	150	207	239	252	0
1900	0	0	0	192	245	280	293	0
2100	0	0	149	229	279	314	329	0
2300	0	0	186	263	310	342	361	0
2500	0	0	221	294	338	369	391	0
2700	0	0	253	324	366	395	419	0
2900	0	0	283	350	391	418	439	0

Table 5.4.c. Maximum ecologically tolerable group size: *Australopithecus anamensis*.

Rain	Temperature (°C)							
(mm)	**0**	**5**	**10**	**15**	**20**	**25**	**30**	**35**
100	0	0	0	0	0	0	0	0
300	0	0	0	0	0	0	0	0
500	0	0	0	0	0	0	0	0
700	0	0	0	0	0	0	0	0
900	0	0	0	0	0	0	0	0
1100	0	0	0	0	0	18	42	0
1300	0	0	0		55	92	114	0
1500	0	0	0	51	118	154	174	0
1700	0	0	0	105	169	207	225	0
1900	0	0	0	152	212	253	270	0
2100	0	0	0	194	251	290	310	0
2300	0	0	0	231	285	322	345	0
2500	0	0	0	265	317	352	377	0
2700	0	0	0	293	347	330	405	0
2900	0	0	0	327	374	406	430	0

Table 5.4.d. Maximum ecologically tolerable group size: *Paranthropus boisei*.

Rain	Temperature (°C)							
(mm)	**0**	**5**	**10**	**15**	**20**	**25**	**30**	**35**
100	0	0	0	0	0	0	0	0
300	0	0	0	0	0	0	0	0
500	0	0	0	0	0	0	0	0
700	0	0	0	0	0	0	0	0
900	0	0	0	0	0	0	0	0
1100	0	0	0	0	15	52	72	0
1300	0	0	0	25	89	122	140	0
1500	0	0	0	85	148	180	196	0
1700	0	0	0	136	195	230	245	0
1900	0	0	0	180	236	273	287	0
2100	0	0	0	219	271	3088	324	0
2300	0	0	173	254	303	337	357	0
2500	0	0	209	286	333	365	388	0
2700	0	0	243	317	361	392	414	0
2900	0	0	273	344	387	416	438	0

Table 5.4.e. Maximum ecologically tolerable group size: *Paranthropus robustus*.

Rain	Temperature (°C)							
(mm)	**0**	**5**	**10**	**15**	**20**	**25**	**30**	**35**
100	0	0	0	0	0	0	0	0
300	0	0	0	0	0	0	0	0
500	0	0	0	0	0	0	0	0
700	0	0	0	0	0	0	0	0
900	0	0	0	0	0	0	10	0
1100	0	0	0	0	39	73	90	0
1300	0	0	0	48	109	140	155	0
1500	0	0	0	106	166	196	209	0
1700	0	0	0	155	211	243	256	0
1900	0	0	112	197	249	283	296	0
2100	0	0	154	234	283	317	331	0
2300	0	0	191	267	313	345	363	0
2500	0	0	225	298	341	371	393	0
2700	0	0	258	327	368	397	418	0
2900	0	0	287	353	393	420	440	0

Table 5.5. Maximum ecologically tolerable group size for hominids for a range of body weight hominids, based on the chimpanzee socioecology model, under different climatic regimes.

Body weight	Temperature (°C)							
(kg)	0	5	10	15	20	25	30	35
30	0	0	1700-2900	1300-2900	1100-2900	900-2900	900-2900	0
40	0	0	2100-2900	1300-2900	1100-2900	1100-2900	1100-2900	0
50	0	0	2700-2900	1300-2900	1300-2900	1100-2900	1100-2900	0
60	0	0	0	1500-2900	1300-2900	1100-2900	1100-2900	0
70	0	0	0	1700-2900	1300-2900	1300-2900	1100-2900	0
80	0	0	0	1900-2900	1300-2900	1300-2900	1100-2900	0
90	0	0	0	2300-2900	1500-2900	1300-2900	1300-2900	0

Table 5.6. Predicted maximum ecologically tolerable group size for the early hominids at current chimpanzee field sites.

Field site	Rainfall (mm)*	Temp. (°C)*	*A.anamensis*	*A.afarensis*	*A.africanus*	*P.robustus*	*P.boisei*
Assirk	1194	29	0	86	36	35	19
Bossou	1779	24	208	240	242	241	228
Budongo	1914	21	225	257	260	259	246
Gombe	959	23	0	0	0	0	0
Kasakati	984	23	0	5	11	9	0
Kibale	1384	20	0	119	123	121	102
Lopé	1522	25	141	177	180	178	164
Mahale	1867	24	188	258	260	259	248
Taï	1534	24	146	183	186	185	169
Lomako	1903	24	401	266	268	267	255
Tumba	2015	24	262	289	291	290	279
Yalosidi	1869	24	229	259	261	260	248
Wamba	2211	24	303	327	329	329	319

*see table 4.9 (p.162) for sources of rainfall and temperature data for each field site.
The line below Taï delimits chimpanzee sites (above) and bonobo sites (below).

Figure 5.7. Maximum ecologically tolerable australopithecine group size (N_{max}) in three habitat types: (a)savanna, (b) woodland and (c) forest. (A.an = *Australopithecus anamensis*; A.afa = *A.afarensis*; A.afr = *A.africanus*; P.rob = *Paranthropus robustus*; P.boi = *P.boisei*).

5.7.a. Savanna habitats

Climate			Australopithecine N_{max}				
altitude (m)	rainfall (mm)	temperature (C)	A.an	A.afa	A.afr	P.rob	P.boi
1035.70	467.87	31.86	0	0	0	0	0
1191.46	431.54	31.86	0	0	0	0	0
330.71	228.09	39.71	0	0	0	0	0
359.05	23.11	37.83	0	0	0	0	0
21.45	598.93	35.61	0	0	0	0	0
21.03	533.15	38.78	0	0	0	0	0
28.96	550.42	39.20	0	0	0	0	0
107.90	498.09	38.50	0	0	0	0	0
1140.49	515.62	35.52	0	0	0	0	0
1310.64	523.49	33.86	0	0	0	0	0
182.88	507.79	33.47	0	0	0	0	0
1197.56	585.98	28.90	0	0	0	0	0
1299.36	420.12	30.19	0	0	0	0	0
1440.49	515.62	35.52	0	0	0	0	0
299.92	497.48	30.30	0	0	0	0	0

5.7.b. Woodland habitats

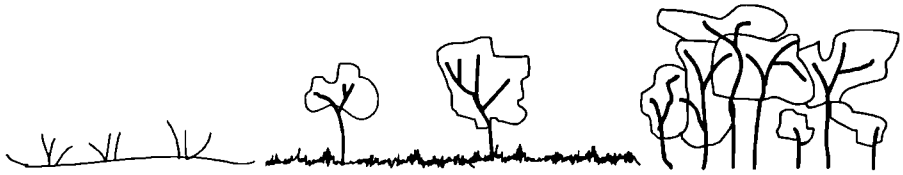
Climate			Australopithecine N_{max}				
altitude	rainfall	temperature	A.an	A.afa	A.afr	P.rob	P.boi
1499.00	1023.29	30.89	0	26	26	24	0
1839.47	1155.79	27.31	21	66	71	69	47
769.92	966.22	27.12	0	0	0	0	0
2.13	1132.84	37.83	0	0	0	0	0
457.20	1207.26	35.61	44	0	7	69	47
85.34	864.87	37.55	0	0	0	0	0
195.07	1194.05	22.16	30	49	54	52	29
1736.45	843.79	27.50	0	0	0	0	0
1527.35	646.94	28.01	0	0	0	0	0
1767.53	817.12	27.21	0	0	0	0	0
1167.69	1527.81	30.21	143	179	182	181	156
1258.52	1344.40	30.61	13	131	21	133	116
99.97	706.37	31.22	0	0	0	0	0
15.59	1232.41	31.89	43	83	86	85	68
342.90	766.06	37.26	0	0	0	0	0

Figure 5.7. continued.

5.7.c. Forest habitats

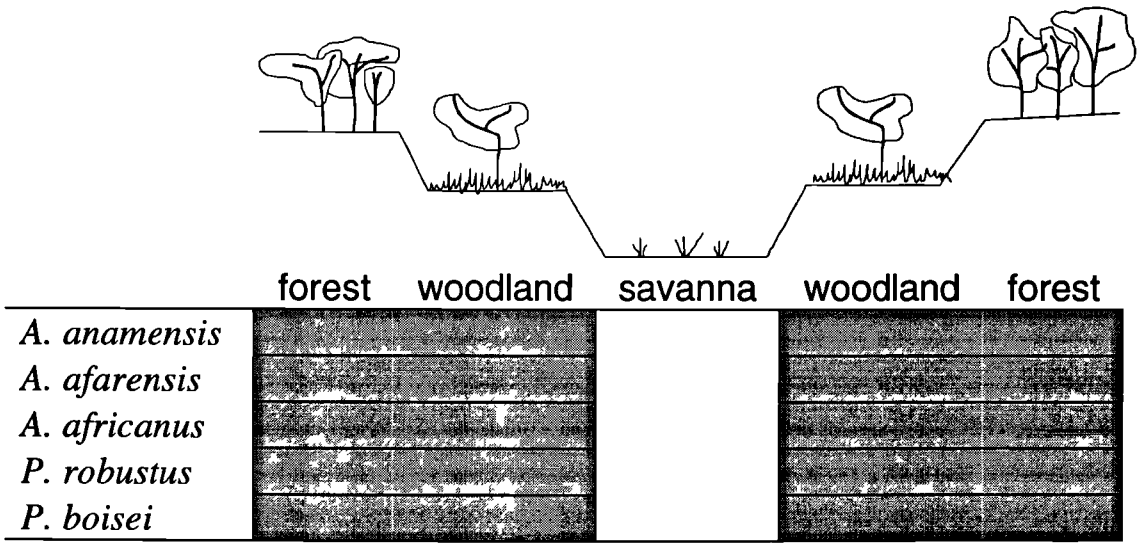
Climate			Australopithecine N_{max}				
altitude (m)	rainfall (mm)	temperature (C)	A.an	A.afa	A.afr	P.rob	P.boi
2154.33	1448.05	27.31	108	156	159	158	140
623.93	1579.88	35.47	0	104	89	105	95
28.96	2958.85	34.95	427	440	440	444	126
2019.30	1667.00	26.88	176	204	207	211	147
64.01	2740.15	38.21	217	256	259	258	242
67.06	2704.59	37.78	212	331	334	254	321
50.90	3228.59	37.50	271	373	374	374	365
16.76	2616.45	37.50	0	241	245	243	226
910.74	1903.98	30.69	236	264	266	265	254
1031.14	1639.32	34.55	125	152	154	153	142
627.88	1740.92	35.57	122	145	147	146	137
2058.40	1753.87	37.10	0	0	0	0	0
619.66	1779.52	35.80	132	155	157	156	147
419.71	1825.75	35.40	145	167	168	168	159
200.86	2069.08	37.73	0	0	0	0	0

Figure 5.6. Mean maximum ecologically tolerable group size for the australopithecines in a range of habitats: savanna, open woodland and forest.



	savanna	open woodland	closed forest
A. anamensis	0	49	197
A afarensis	0	89	229
A. africanus	0	102	230
P. robustus	0	87	225
P. boisei	0	78	192

Figure 5.7. Schematic diagram of African rift habitats, and mean australopithecine group sizes in these differenent habitat types.



Bars indicate those habitats hominds can occopy, based on maximum ecologically tolerable group size predictions in the habitat types.

5.3.5. Predictions of the model for N_{max} at fossil locations

The predictions of the model so far have focussed on modern habitat types. These results are important for comparing with the predictions for habitat types at the fossil sites during the time of their occupation by the early hominids. Precise estimates of rainfall and temperature for each of the fossil sites are less readily available. Dunbar (1992*e*) compiled a table of habitat variables for the extinct papioninds, using information provided by Shipman & Harris (1988). The same method is followed here, supplementing data where it is unavailable by adjusting current climate for the fossil location and adjusting for differences in global temperature over time (see Prentice & Denton 1988). The predicted palaeoenvironmental data for each fossil location is tabulated in table 5.8.

Table 5.8. Australopithecine N_{max} for fossil sites.

South African sites

Species	Makapan.	Swartkrans	Kromdraai	Sterkfontein	Taung
A.anamensis	0	0	0	0	0
A.afarensis	0	0	0	0	0
A.africanus	0	0	0	0	0
P.robustus	0	0	0	0	0
P.boisei	0	0	0	0	0
Rainfall(mm)	700	800	800	800	750
Temp. (°C)	23.2	20.8	20.8	20.8	25.0

East African sites

Species	Kanapoi	Hadar	Laetoli	Omo	Turkana	Olduvai
A.anamensis	0	0	0	0	0	0
A.afarensis	0	0	0	0	0	65
A.africanus	0	0	0	0	0	57
P.robustus	0	0	0	0	0	55
P.boisei	0	0	0	0	0	35
Rainfall(mm)	850	700	750	640	300	1100
Temp. (°C)	25.5	26.6	24.5	20.0	25.0	25.4

Large number of zero group sizes reflects several features of the chimpanzee model. Firstly the model was constructed from populations occupying regions with higher rainfall values than those predicted above (table 5.8). Secondly, further evidence comes from the analysis investigated maximum ecologically tolerable group sizes in different

extant habitat types. The results of this analysis suggest that further modifications to the chimpanzee model are required if its predictions are to be extended to habitats with lower mean annual rainfall than it was constructed from. The estimates for mean annual rainfall for the fossil sites may be too low, particularly given the habitat types they describe. Further assessment of their accuracy will be possible when more concrete palaeoenvironmental data become available.

5.3.6. Discussion

The model presented here is a first attempt to use the time budget socioecology model to predict the maximum ecologically tolerable group sizes. The model on the extant chimpanzees predicted very well the geographic distribution of the extant chimpanzees, with this firm grounding in extant behavioural ecology, the model was extended to the extinct early hominids.

The chimpanzee socioecology model was used, under the assumption that the chimpanzees may be the most appropriate modern analogue for the early hominids. However, the soecioecological models presented in this study are not constructed to be species specific, but to be habitat specific. The australopithecine model presented here assumes that the australopithecines occupied the same ecological 'grade' as the extant chimpanzees, but differed in key biological variables, notably body weight. The range of australopithecine body weights predicted from McHenry's (1994) equations place them within the range of variation of body weights for the extant chimpanzees (see table 4.22, p. 188) with the exception of *A. anamensis*.

Further adaptations to the model would be needed to be made to incorporate the locomotor adaptations of the australopithecines. *Australopithecus* had arboreal adaptations (Susman *et al.* 1985; Tuttle 1981). The energetic efficiency of locomotion is thought to be important in the evolution of social structure (Rodman & McHenry 1980).

Opinion is divided as to which species might have been the result of aridification pressures: *Australopithecus*, *Paranthropus* or *Homo*? (Reed 1997).

The geographic distribution of ancestral populations of African apes and hominids was constrained to tropical Africa and its lowland forests (Bromage & Schrenk 1995). Rifting in east Africa led to a reduction of the forests and an increase in open grasslands in east Africa 8-9mya (Pickford 1991). Furthermore, distribution drift of tropical forest left more wooded savanna in its wake (Andrews 1981). Towards the end of the Miocene, climatic conditions were at their most extreme, arboreal hominids were peripheralised to the forests in the rain shadows of the developing African Rift Valley. The open woodlands provided habitats for the early arboreal hominids, separated by non-arboreal terrain. Bromage & Shrenk (1995) hypothesise that the early *A. ramidus* (White *et al.* 1994) (or its ancestor *Ardipithecus*) arose in a tropical east African environment. *A. ramidus* is thought to be associated with closed woodlands (WoldGabriel *et al.*1994). By 4.0mya, *A. afarensis* was distributed in wider riparian habitats and open woodlands, dispersing through the riparian corridor connecting east and southern Africa (Bromage Schrenk & Juwayeyi 1995). By around 2.8mya, Africa became cooler and drier climaxing at ca. 2.5mya (Bonnefille 1976; Prentice & Denton 1988; Vrba *et al.*, 1985*b*, 1989). Global aridification increased the rate of faunal turnover (Vrba 1992). During the period between 2.8mya and 2.5mya, the increased aridity resulted in increasingly open habitats, separated by narrow areas of riverine forest. The megadont hominid species with specialisations for a harder diet were better able to survive in the more open savanna habitats. The increasing aridity is thought responsible for the separation of the lines of *A. afarensis* into *Paranthropus* and *Homo* lineages by ca. 2.5mya (Vrba 1988).

The first *Paranthropus* (=*Australopithecus*) *aethiopicus* (e.g. Walker *et. al.* 1986; Kimbel *et al.* 1988) was thought to have relied on fruits during the dry season but also had dentition adapted for harder food sources in open habitats. *P. boisei* had more pronounced megadonty thought to be an adaptation for tougher vegetation in woodland savanna. Similar to the analyses presented in this thesis, the predictions of Bromage & Schrenk (1995) are not concerned with the taxonomic level of regional differences but to the consequences of these differences for the distribution of early hominids from a

biogeographic perspective. *P. robustus* has dental characteristics which distinguish it from earlier *A. africanus*; a powerful jaw, thick enamel, large molars and reduced anterior teeth. These characteristics of *P. robustus* may be adaptations for crushing and grinding (e.g. see Walker 1981; Grine 1981).

The model presented here adjusts one simple variable, body weight and does not therefore take into account alternative strategies extinct species may have had for adapting to local habitat conditions. This may be particularly true with respect to the robust australopithecines, who in the model presented here have the same habitat preferences as the gracile australopithecines. The results presented here represent the first attempt to extend the maximum ecologically tolerable group size approach to modelling the behavioural ecology of the early hominds. The use of current climate data to characterise habitat types relies on the assumption that the same climatic conditions determined vegetation structure today as they did in the plio-Pleistocene. As more detailed palaeo-climate predictions become available, these will provide important inputs for modelling further the habitat preferences of the early hominids.

CHAPTER 6. CONCLUDING DISCUSSION

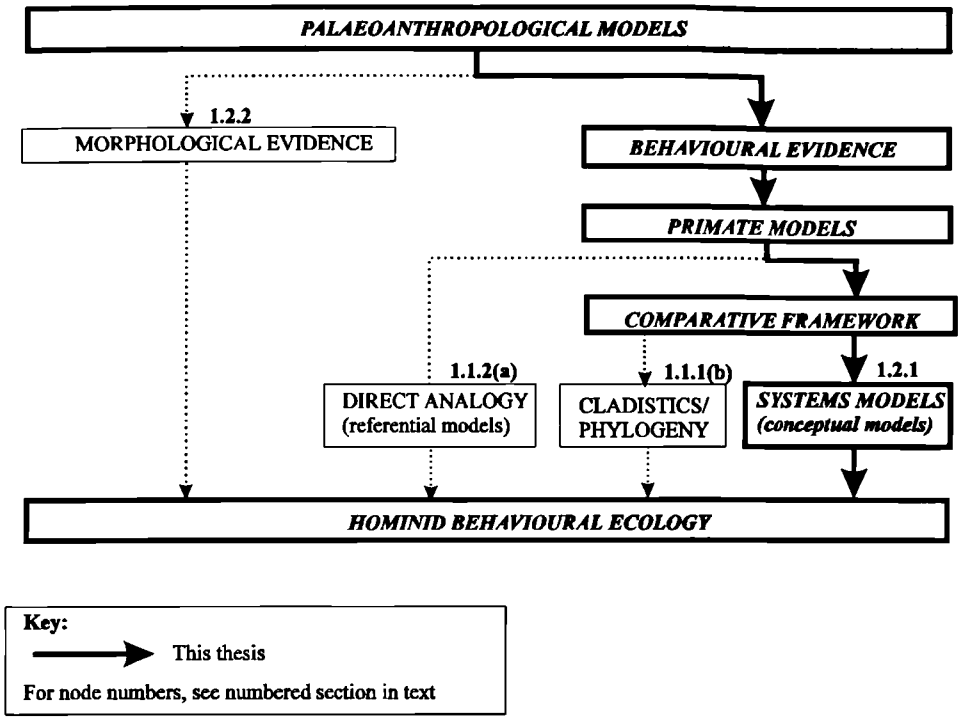
CHAPTER 6. CONCLUDING DISCUSSION

6.1. Theoretical framework of the research

The results of studies on the behaviour and ecological context of extant primates are important in developing a fuller understanding of our early ancestors. Despite ever increasing information from skeletal material, as well as some degree of behavioural data from trace fossils (e.g. hominid trackways and tools), fossil evidence alone is insufficient to examine questions on the behavioural and ecological adaptations of the early hominids.

At present there exists no established method for investigating the behaviour of extinct taxa. This research aims to construct a theoretical framework which allows the investigation of the behavioural ecology of extinct hominids. The principal aim of this study was to use behavioural data from extant primates to establish firm framework of the relationships between behaviour and environment, which could be used as a predictive tool for extinct species. Due to the adaptive flexibility of a lineage through time, palaeobehavioural models should be built in an evolutionary context (Tooby & DeVore 1987). The data for these models come from extant primates. Species used in the model were chosen on conceptual, ecological grounds, rather than as direct analogues and included baboons (*Papio* spp.) and chimpanzees (*Pan* spp.). These models however, should not be deterministic, but flexible enough to reproduce the fine-tuned responses of animals to the ecological and behavioural variables that influence their behaviour. Deterministic, or referential models use extant primate data as direct analogies. These models are considered here not flexible enough for use with extinct taxa (see Moore 1996 for a review). The pathway followed in developing predictive models in this thesis is illustrated in the diagram below (fig. 6.1)

Figure 6.1. Schematic diagram of the categories of primate derived models used to reconstruct aspects of hominid behavioural ecology (node numbers refer to sections in chapter 1).



This study has focused on systems models, which are a specific example of the "conceptual" modelling approach advocated by Tooby & deVore (1987). Systems models exploit the fact that there are well established relationships between behavioural and ecological variables (see Rubenstein & Wrangham 1986). These models quantify these relationships and identify causal relationships between the components of a "system". The "system" in this context is the social system of extant or extinct primates (see section 1.2.).

6.2. Overview of the thesis

The important components in the systems models in this study are ecological and behavioural variables. Multiple regression, one of the principal statistical techniques used in these models, requires discrete well characterised independent variables (see 3.4.2). Restricted and well defined ecological variables whose relationships are well known were therefore required. Climatic variables influence the distribution and behaviour of animals directly (through thermal stress) and indirectly (e.g. availability and

quality of food, shelter and water supply). Site-specific ecological data for primate field sites is rarely in a form that is *directly comparable* between sites. Therefore indirect climatic indices of habitat type were sought. Using data from large number of sub-Saharan weather stations, the analyses in chapter 2 revealed that three key variables were sufficient to characterise habitat type. These three variables were; temperature, mean annual rainfall and seasonality of rainfall. A variety of seasonality indices were investigated to find those that were the most suitable for characterising seasonality over the widest range of habitat types. Simpson's index and the new index (DIV) described in section 2.2.3 were found to be most representative over the widest range of habitat types. It was found that quantitative equations between environmental variables were constructed from both Old World and New World climate data, and were found to be equally predictive. The quantitative relationships between environmental variables developed here were used in the models developed in chapters 3 and 4, and on platyrrhine primates (Pastor-Nieto & Williamson *in review*). The equations defining these relationships will serve as useful constants for use in the further development of systems models of primate socioecology, and with caution to socioecological models on extinct taxa (see section 2.5).

To survive within a given environment, an animal must develop behavioural, physiological or morphological adaptations, which allow it to cope with the specific ecological constraints of that environment. These behavioural responses include changes in time budgets, shifts in home range and changes in the length of the active period. The systems models presented in chapters 3 and 4 quantifiably examine the factors affecting variations in group size. These variations are a consequence of optimisation decisions by animals in response to environmental variability. The model presented in chapter 3 is an extension of previous models of group size in baboons (Dunbar 1992*b*, 1994; see reply by Bronikowski & Altmann 1996). The model was further refined in Dunbar (1996), updating behavioural data, and using the ecological equations from this study (chapter 2). The reanalysis was conducted in the light of recent criticisms of the original model (Bronikowski & Altmann 1996). These criticisms focused on three key areas; the validity

of using step-wise multiple regression, the accuracy and duration of climate data, and the time budget data used in the original model. With careful screening of the data for violations of the assumptions of stepwise regression, any possibly underlying biases were minimised. The equations were also shown to be biologically plausible, which further supported to their use. When long-term and short-term climate data were compared, the proximity of the weather station to the primate field site was found to be more important. A mixture of long-term and short-term climate data were used, emphasising the proximity of the climate source to the primate field site. These data were most accurate in predicting the time budgets of an independent sample of baboons. The availability of long-term term, site-specific climate data is therefore a priority for further comparative analyses between primate populations. The baboon model was found to be robust, since the equations remained highly predictive when newly available time budget data was incorporated. This is an important criterion for a successful model, in that it should be flexible enough to incorporate new data when they become available.

Models developed on baboons were subsequently extended to the chimpanzees (see chapter 4). Whilst chimpanzees were selected as conceptual models, there were aspects of their selection that were based on more referential grounds. The early hominids, specifically the gracile australopithecines, are thought to be of similar size, encephalisation, habitat and diet to the extant chimpanzees. As the ultimate aim of this study is to extrapolate from models of extant primate socioecology to the early hominids, the model species should therefore have as great a similarity to these hominids as possible.

In the construction of the model on baboon socioecology, long-term and accurately sited climate data was found to be important. Therefore care was taken in the compilation of climate data for the chimpanzee field sites. Proximity of the climate data to the field site was considered more important than sites with long-term climatic data, as shown in the baboon models in chapter 3. Once climate data had been compiled from long-term sources, chimpanzee and bonobo field sites could be compared. When the field sites are compared, particularly with respect to the seasonality indices developed in

chapter 2, Mount Assirik emerged as the most seasonal site but not the driest. Budongo was found to be the driest field site overall, whereas previous work (e.g. McGrew *et al.* 1981) had considered Gombe to be drier.

The sample size of chimpanzee time budgets was significantly smaller than that available for the baboons. Therefore great care was taken not to violate the assumptions of the statistical tests. The predicted maximum ecologically tolerable group sizes of chimpanzees matched those of observed populations. Because *comparative* data were scarce, an independent sample could not be used to test the models predictions. Instead the model was written in reverse, so that climatic variables from 70 weather stations in sub-Saharan Africa were used as inputs. Chimpanzees were predicted to live in the geographic regions chimpanzees are currently found. However the model also predicted chimpanzee populations to exist in areas outside their current distribution. These occurrences may be explained by a variety of factors. Habitat conditions present today in Madagascar may be suitable for chimpanzees. The pre-Neogene separation of Madagascar from mainland Africa precluded its colonisation by non-human hominines. However, the Indri (*Indri indri*), a large bodied arboreal lemur, present in Madagascar today appears to occupy a similar ecological niche to the chimpanzees in Africa. Conditions predicted to be suitable for chimpanzees in Southeast of Africa exist largely in upland forest areas separated from chimpanzee ranging areas by surrounding dryland savanna. Local variations in topography along the zone of the Great Rift Valley create local areas sufficiently wet to support forests suitable for chimpanzees. However the dynamic nature of the rift valleys' geological history has meant that either these environments are too ephemeral, or have remained isolated through time to support chimpanzees. It is possible however that chimpanzees, or similar primates either exist or have existed in this area in the recent past, possibly confirmed by the sightings of small "furry ape-men" (cited in Huevelmans 1965: 227) in southern Tanzania and Mozambique. These observations support the models' prediction that chimpanzees exist in these more southerly distributions.

The analyses that could be conducted in chapter 4 were restricted by the availability of sufficiently detailed *comparable* data between chimpanzee and bonobo field sites. The lack of detailed data, particularly on bonobos was recently highlighted (Thompson-Handler *et al.* 1995). An analysis of population viability was conducted to predict the effect of a range of factors (e.g. unit group size, hunting pressure and the carrying capacity of the habitat) but again was restricted by the amount of data available. Additional information is currently being conducted on classifying habitat types in chimpanzee field sites using satellite images (Thompson-Handler *et al.* 1995). This information is essential since *comparable* detailed behavioural and ecological data is central to the construction of systems models. However, simulation type models have been conducted on chimpanzees (e.g. te Boekhorst & Hogeweg 1994*a*, *b*). However, these models were not considered suitable for a study of this type. These models investigated whether grouping patterns similar to chimpanzees were reproducible among non-territorial, unrelated artificial entities. The complex interaction between the artificial entities ('CHIMPS') and the habitat structure in the model, produced grouping patterns very similar to those of real chimpanzees. This modelling technique was bottom-up in approach in contrast to the top-down systems models advocated in this study (see section 1.1.2). The grouping patterns resulting from the 'CHIMP' models resulted from the direct interaction between the subjects and environment, without assuming any additional benefits or costs of group living. The systems models in this study built in assumptions about the costs and benefits of group living, and related ecological variables to those group size constraints (see section 3.2.1). The approaches used in evolutionary ecology focus on optimal traits to provide a mechanistic understanding of behavioural patterns.

The assumption running through the models on chimpanzees was that environmental constraints affected chimpanzee group size. Models of primate group size have been constructed on the assumption that there is a non-linear relationship between group size and the costs of group membership. This is due to the three fold costs of group size (predation risk, food availability and distribution) being affected by climate in

different ways (see section 4.7.1). Each parameter could be related simply to an environmental variable (mean annual rainfall). The correlation between the costs of group size and rainfall assumed that forest cover was related to rainfall. However, there is very little data on actual forest cover at chimpanzee field sites that is in a comparable form between sites. Different study sites have different priorities for research, and therefore have recorded different variables. This is partly a consequence of the observation conditions in the forest, here continuous behavioural records are difficult to observe. Those forest cover data that were available were correlated with mean annual rainfall, and the relationship was confirmed. However, for the chimpanzee sites with good data high rainfall habitats appeared to have the lowest forest cover, the opposite to that predicted. This result was thought to be due to deforestation in those sites where data were recorded. The party size data used were potentially biased since different definitions for parties exist between researchers at different field sites. Although observation conditions partly contribute to different definitions of party size, a unified definition would seem to be a priority for further comparative work between chimpanzee communities. The relationships between the costs of group size and rainfall were supported by the simple non-linear regression equation relating party size to mean annual rainfall for chimpanzees and bonobos (see 4.7.4).

With the successful extension of the systems modelling approach to modelling maximum ecologically tolerable group size in chimpanzees, the results could be compared with those obtained previously on baboons (chapter 2 this study; Dunbar 1992*b*; 1994; Bronikowski & Altmann 1996) and gelada baboons (Dunbar 1992*a*). Baboons (*Papio* spp.) were selected for initial study because more long-term field data were available on this genus than any other primate taxon. The modelling approach was further extended to the gelada baboons (*Theropithecus gelada*). Although gelada have only been studied at three sites, they are closely related to *Papio* baboons, and therefore their physiological responses to environmental constraints were thought to be similar (Dunbar 1996). Nevertheless, baboons are principally frugivores, and gelada graminovores (grazers). This dietary niche separation allowed the examination of the

influence of dietary niche to various components of the "system" (social system). Chimpanzees were used to further extend the baboon models for two reasons. Firstly that chimpanzees are a more realistic model for the early hominids. Secondly chimpanzees they also represent an interesting extreme in ecological and life history adaptation. Chimpanzees' diet (ripe fruit frugivores), is more restricted than that of the baboons and therefore provides further insight into the influence to the model of dietary niche. On comparison of the maximum ecologically tolerable group sizes, the niche separation of chimpanzees, gelada and chimpanzees had a dietary basis, reflecting the way their preferred diet responds to climatic variables. Gelada live in cool habitats, due to their dependence on high altitude grasslands. Since temperature correlates with altitude (see chapter 2), the altitudinal distribution of baboons and gelada reflects the temperatures for which these taxa are most adapted. The chimpanzee distribution was found to be a mirror image of that for baboons, rainfall being the main climatic variable separating these two taxa. This may reflect chimpanzees' preference for tree-based feeding sites, in contrast to baboons for feeding in the shrub layer. The feeding time equations for the three taxa illustrated further the way that the three taxa's niche separation could be traced back to dietary differences. The importance of diet, as a distinguishing between taxa in these models warrants further study. The systems models in this thesis have been from a top-down modelling approach, whereas further extensions of the model could be envisaged from the bottom-up. Using first principles to build up individuals dietary, and thus feeding time constraint (chapter 5).

The systems models in this thesis centre on optimality decisions that are well established by long-term field studies on the behavioural ecology of primates. Whilst these optimality decisions are assumptions of the model, one important use of the models is to draw attentions to key processes which could warrant further field study. With well established ecological relationships, a well supported methodology, and extension of the systems models with chimpanzee data, we are in a much stronger position to extrapolate the models beyond the current time frame and ecological context. Given the results of the models developed in this study, in the following section I suggest how the

development of the conceptual model for the early hominids should proceed, and which data would be required.

6.3. The development of a conceptual model for the early hominids

The behavioural ecological perspective for reconstructing the behaviour of the early hominids relies on the theory of ecological uniformitarianism (see Gifford-Gonzalez 1991). The models on the chimpanzees were developed with the australopithecines in mind as focus species. The preliminary conceptual model for the early hominids outlined in chapter 5 (section 5.3.1) represents the first attempt to extend the models of primate socioecology based on extant primate time budgets, to the extinct early hominids.

Although the model developed in this study was largely constructed with the aim of reconstruction australopithecine socioecology, it may also have implications to various other fields of palaeoecological study. By using the model 'in reverse', it may be of use in delimiting the factors contributing to the extinction of a species, or those necessitating changes to the species in order to survive which result in a speciation event. The model may also be used to predict whether the palaeoenvironment at a particular fossil site was suitable for hominid habitation, and hence whether unproductive fossil sites yield no hominid remains because hominids could not have lived in that area, or whether the lack of remains is purely due to ecological or taphonomic factors. Additionally, the model may be applicable to the palaeoecological analysis of other extinct animals, even those with no close living relatives, so long as the limitations of the model are fully appreciated. This is possible as the model relies of variables which are often indirectly obtainable from fossil material; diet, body mass and a knowledge of the general physiology of that animal group.

To summarise, the ecological context, functional morphology and evolutionary history of the australopithecines are well characterised, and these data will provide the testing ground for further extensions of the models presented in this study. The key point in the structure of these models was that they should be firmly grounded in the ecological context of the species being modelled. This is an important criteria to carry

forward in the extension of models in a palaeoenvironmental context (Oliver *et al.* 1994). The linear programming models adopted in this study for modelling the socioecology of extant primates satisfy the criteria for a conceptual model for extinct taxa. Conceptual models use sets of theories and concepts. In these models, well established relationships between behavioural and environmental variables. Primate social systems are characteristically variable, therefore a more flexible approach than is possible from conventional comparative referential models is advocated here.

Models of socioecology may represent the *only* opportunity to explore in detail the complexity of social strategies of extinct taxa in an evolutionary framework.

REFERENCES

REFERENCES

Aiello, L. C., & Dunbar, R. I. M. 1993. Neocortex size, group size and the evolution of language. *Curr. Anthropol.*, **34**, 184-193.

Aiello, L. C., & Wheeler, P. 1994. The expensive tissue hypothesis: The brain and digestive system in human and primate evolution. *Curr. Anthropol.*, **36**, 199-221.

Aiello, L. C. & Wood, B. A. 1994. Cranial variables as predictors of hominine body mass. *Am. J. Phys. Anthropol.*, **95**, 409-426.

Alexander, R. D. 1974. The evolution of social behaviour. *Ann. Rev. Ecol. Syst.*, **5**, 325-383.

Altmann, J. 1980. *Baboon Mothers and Infants*. Cambridge: Harvard University Press.

Altmann, J. 1983. Costs of reproduction in baboons (*Papio cynocephalus*). In: *Behavioural Energetics* (Ed. by W. P. Aspey & S. I. Lustick), pp. 67-88. Columbus: Ohio State University Press.

Altmann, J., Hausfater, G. & Altmann, S. A. 1985. Demography of Amboseli baboons, 1963-1983. *Am. J. Primatol.*, **8**, 113-125.

Altmann, S. A. & Altmann, J. 1970. *Baboon Ecology*. Basel: Karger.

Amaral, L. Q. 1996. Loss of body hair, bipedality and thermoregulation. Comments on recent papers in JHE. *J. Hum. Evol.*, **30**, 357-366.

Andrews, M. W. & Rosenblum, L. A. 1988. Relationship between foraging and affilliative social referencing in primates. In: *Monographs in Primatology, Vol. 11. Ecology and Behaviour of Food-Enhanced Primate Groups* (Ed. by Fa, J. E. & Southwick, C. H), pp. 247-268. New York: Alan Riss.

Andrews, P. 1981. Hominoid habitats of the Miocene. *Nature*, **289**, 749.

Andrews, P., & Aiello, L. 1984. An evolutionary model for feeding and positional behaviour. In: *Food Acquisition and Processing in Primates* (Ed. by D. Chivers, B. Wood, & A. Bilsborough), pp. 429-466. New York: Plenum Press.

Andrews, P., & Martin, L. 1991. Hominoid dietary evolution. *Phil. Soc. R. Soc. Lond. B.*, **334**, 199-209.

Anon. 1984. *Africa, the Atlantic Ocean South of 35°N and the Indian Ocean (Met. 0.85.d.). Tables of Temperature, Relative Humidity, Precipitation and Sunshine for the World.* Her Majesties Stationary Office (H.M.S.O): London.

Anon, 1988. Rainfall records, Directorate of Meteorology, Dar es Salaam, Tanzania.

van den Audenaerde, D. F. E. T. 1984. The Tervuren Museum and the pygmy chimpanzee. In: *The Pygmy Chimpanzee: Evolutionary Biology and Behavior* (Ed. by R. L. Susman), pp. Plenum: New York.

Badrian, A., & Badrian, N. 1984. Social organization of *Pan paniscus* in the Lomako forest, Zaire. In: *The Pygmy Chimpanzee* (Ed. by R.Susman), pp. 325-346. New York: Plenum Press.

Baer, D., & McEaechron, D. L. 1982. A review of selected sociobiological principles: application to hominid evolution. I. The development of group social structure. *J. Social. Biol. Struct.*, **5**, 69-90.

Bailey, H. P. 1979. Semi-arid climates: their definitions and distribution. In: *Agriculture In Semi-Arid Environments* (Ed. by A. E. Hall, G. H. Canell & H. W. Lawton), pp. 73-97. Berlin: Springer.

Baldwin, P.J., McGrew, W.C., & Tutin, C.E.G. 1982. Wide-ranging chimpanzees at Mt. Assirik, Senegal. *Int. J. Primatol.*, **3**, 367-385.

Baldwin, P.J., Sabater Pi, P.J., McGrew, W.C., & Tutin, C.E.G. 1981. Comparisons of nests made by different populations of chimpanzees (*Pan troglodytes*). *Primates*, **22**, 474-486.

Barnard, C. J. 1980. Flock feeding and time budgets in the house sparrow (*Passer domesticus*). *Anim. Behav.*, **28**, 295-309.

Barnard, C. J., Thompson, D. B. A. & Stephans, H. 1983. Time-budgets, feeding efficiency, and flock dynamics of mixed species flocks of lapwings, golden plovers, and gulls. *Behaviour*, **80**, 44-69.

Barrett, L., Dunbar, R. I. M. & Dunbar, P. 1995. Mother-infant contact as a contingent behaviour in gelada baboons. *Anim. Behav.*, **49**, 805-810.

Bartholemew, G. A. 1958. The role of physiology in the distribution of terrestrial vertebrates. In: *Zoogeography* (Ed. by C. L. Hubbs), pp. 81-95. Washington D.C: American Association for the Advancement of Science, Publication No. 51.

Barton, R. A. 1989. *Foraging Strategies, Diet and Competition in Olive Baboons.* Ph.D. Thesis, University of St. Andrews.

Barton, R. A., Whiten, A., Strum, S. C., Byrne, R. W. & Simpson, A. J. 1992. Habitat use and resource availability in baboons. *Anim. Behav.*, **43**, 831-844.

Beauchamp, G. & Cabana, G. 1990. Group size variability in primates. *Primates*, **31**, 171-182.

Begun, D. R. 1994. Relations among the great apes and humans: New interpretations based on the fossil great ape Dryopithecus. *YrBk. Phys. Anthropol.*,

Behrensmeyer, A. K. 1982. Geological context of human evolution. *An. Rev. Earth Planet Sci.*, **10**, 39-60.

Bell, R. H. V. 1982. The effect of soil nutrient availability on community structure in African ecosystems. In: *Ecology of Tropical Savannas* (Ed. by B. J. Huntley & B. H. Walker), pp. 193-216. Berlin: Springer-Verlag.

Belovsky, G. E. 1994. How good must models and data be in ecology? *Oecologia*, **100**, 475-480.

Berger, J. 1988. Social systems, resources and phylogenetic inertia: an experimental test and its limitations. In: *The Ecology of Social Behaviour* (Ed. by C. N. Slobodchikof), pp. 157-186. London: Academic Press.

Binford, L. R. 1977. *For Building in Archaeology.* New York: Academic Press.

Binford, L. R. 1981. *Bones, Ancient Men and Modern Myths.* New York: Academic Press.

Blumenberg, B. 1981. Observations on the paleoecology, population structure and body weight of some Tertiary hominoids. *J. Hum. Evol.*, **10**, 543-564.

Blumenberg, B. 1983. The evolution of the advanced hominid brain. *Curr. Anthropol.*, **24**, 589-623.

Blumenberg, B. 1984. Allometry and evolution of tertiary hominoids. *J. Hum. Evol.*, **13**, 613-676.

Blumenberg, B. 1985. Population characteristics of extinct hominid endocranial volume. *Am. J. Phys. Anthropol.*, **68**, 269-280.

Blumenschine, R. J. 1986. *Early Hominid Scavenging Opportunities: Implications of Carcass Availability in the Serengeti and Ngorongoro Ecosystems.* Oxford: British Archaeological Reports International Series 283.

Blumenschine, R. J. 1987. Characteristics of an early hominid scavenging niche. *Curr. Anthropol.*, **28**, 383-407.

Blumenschine, R. J. 1991. Hominid carnivory and foraging strategies, and the socio-economic function of early archaeological sites. *Phil. Trans. R. Soc. LondB,* **334**, 211-221.

Blumenschine, R. J., & Masao, F. T. 1991. Living sites at Olduvai Gorge, Tanzania? Preliminary landscape archaeology results in the baasal Bed II lake margin zone. *J. Hum. Evol.*, **21**, 451-462.

Blumenschine, R. J., Cavallo, J. A., & Capaldo, S. D. 1994. Competition for carcasses and early hominid behavioral ecology: a case study and conceptual framework. *J. Hum. Evol.*, **27**, 197-213.

Boesch, C. 1991. The effects of leopard predation on grouping patterns in forest chimpanzees. *Behaviour*, **117**, 221-242.

Boesch, C. & Boesch, H. 1989. Hunting behaviour of wild chimpanzees in the Tai National Park. *Am. J. Phys. Anthropol.*, **78**, 547-573.

Bonnefille, R. 1976. Palynological evidence for an important change in the vegeatation of the Omo Basin between 2.5 and 2 million years ago. In: *Earliest Man and Environments in the Lake Rudolf Basin* (Ed. by Y. Coppens, F. C. Howell, G. L. I. Issaac & R. E. F. Leakey), pp. 421-431. University of Chicago Press: Chicago.

Bonnefille, R. 1984. Cenozoic vegetation and environments of early hominids in East Africa. In: *The Evolution of the East Asian Environment* (Ed. by R. O. Whyte), pp. 579-612. Hong kong: Centre of Asian Studies, University of Hong Kong.

Bonnfille, R. & Vincens, A. 1985. Apport de la palynologie à l'environment des Hominidés d'Afrique orientale. In: *L'Environment des Hominidés au Plio-Pléistocène*, pp. 237-278. Masson: Paris.

Bourliére, F. & Hadley, M. 1983. Present-day savannas: an overview. In: *Ecosystems of the world, 13, Tropical Savannas* (Ed. by F. Bourliére), pp. 1-17. Amsterdam: Elsevier.

Bowden, B. N. 1964. The dry seasons of inter-tropical Africa and Madagascar. *J. Trop. Geogr.* **19**, 1-3.

Box, E. O. 1981. *Macroclimate and plant forms: an introduction to predictive modelling in phytogeography.* The Hague: Junk.

Bromage, T. G. & Schrenk, F. 1995. Biogeographic and climatic basis for a narrative of early hominid evolution. *J. Hum. Evol.*, **28**, 109-114.

Bronikowski, A. M., & Altmann, J. 1996. Foraging in a variable environment: weather patterns and the behavioural ecology of baboons. *Behav. Ecol. Sociobiol*, **39**, 11-25.

Bronikowski, A. M. & Webb, C. 1996. Appendix: A critical examination of rainfall variability measures used in behavioral ecology studies. *Behav. Ecol. Sociobiol.*, **39**, 27-30.

Bultot, F. 1971. Rwanda and Burundi. In: *Climates of Africa, World Survey of Climatology 10* (Ed. by J. F. Griffiths), pp. 349-368. Amsterdam: Elsevier.

Bunn, H. T., & Ezzo, J. A. 1993. Hunting and scavenging by Plio-Pleistocene hominids: nutritional constraints, archaeological patterns, and behavioural implications. *J. Archaeol. Sci.*, **20**, 365-398.

Bunn, H. T., & Kroll, E. M. 1986. Systematic butchery by Plio/Pleistocene hominids at Olduvai Gorge, Tanzania. *Curr. Anthopol.*, **27**, 431-452.

Butynski, T. M. 1990. Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high- and low-density sub-populations. *Ecol. Monog.*, **60**, 1-26.

Bygott, D. 1974. *Agonistic Behaviour in Wild Chimpanzees*. PhD Thesis, University of Cambridge.

Byrne, R. W. 1981. Distance vocalisations of Guinea baboons (*Papio papio*) in Senegal: an analysis of function. *Behaviour*, **78**, 283-312.

Caldecott, J. O. 1986. Mating patterns, societies and the ecogeography of macaques. *Anim. Behav.*, **34**, 208-220.

Calder, W. A. 1984. Size, Function and Life History. Cambridge: Harvard University Press.

Cameron, D. W. 1993. The pliocene hominid and protochimpanzee behavioral morphotypes. *J. Anthropological Archaeology*, **12**, 386-414.

Caraco, T. 1979*a*. Time budgeting and group size: A theory. *Ecology*, **60**, 611-617.

Caraco, T. 1979*b*. Time budgeting and group size: A test of theory. *Ecology*, **60**, 618-627.

Carr, C. J. 1976. Plant ecological variation and pattern in the lower Omo basin. In: *Earliest Man and the Environments in the Lake Rudolf Basin* (Ed. by Y. Coppens, F. C. Howell, G. L. L. Isaacs & R. Leakey), pp. 432-467. Chicago University Press: Chicago.

Cartmill, M. 1990. Human uniqueness and theoretcal content in paleoanthropology. Int. J. Primatol., **11**, 173-192.

Caughley, G., Grice, D., Barker, R. & Brown, B. 1988. The edge of the range. *J. Anim. Ecol.*, **57**, 771-785.

Cerling, T. E. 1992. Development of grasslands and savanna in East Africa during the Neogene. *Palaeogeogr. Palaeoclimat. Palaeoecolol.*, **97**, 241-247.

Chaplin, G., Jablonski, N. G. & Cable, N. T. 1994. Physiology, thermoregulation and bipedalism. *J Hum. Evol.*, **27**, 497-510.

Chapman, C. A. 1990. Ecological constraints on group size in three species of neotropical primates. *Folia. Primatol.*, **55**, 1-9

Chapman, C. A., White, F. J. & Wrangham, R. W. 1994. Party size in chimpanzees and bonobos: a reevaluation of theory based on two similarly forested sites. In: *Chimpanzee Cultures* (Ed. by R. W. Wrangham, W. C. McGrew, F. B. M. de Waal & P. Heltne), pp. 41-57. Cambridge, MA: Harvard University Press.

Chapman, C. A. & Lefebvre, L. 1990. Manipulating foraging group size: spider monkey food calls at fruiting trees. *Anim. Behav.*, **39**, 891-896.

Chapman, C.A., & Wrangham, R.W. 1993. Range use of the forest chimpanzees of Kibale. Implications for the understanding of chimpanzee social organization. *Am. J. Primatol.*, **31**, 263-273.

Charles-Dominique, P. 1977. *Ecology and Behaviour of Nocturnal Prosimians.* Columbia Univ. Press: New York.

Chong, L. S. D., Mougin, E., & Gastellu-Etchegorry, J. P. 1993. Relating the Global Vegetation Index to net primary productivity and actual evapotranspiration over Africa. *Int. J. Remote Sensing*, **14**, 1517-1546.

Clarke, A. & Wrangham, R. W. 1994. Chimpanzee arrival pant hoots: do they signify food or status? *Int. J. Primatol.*, **15**, 185-206.

Clinebell II, R. R., Phillips, O. L., Gentry, A. H., Stark, N., & Zuuring, H. 1995. Prediction of neotropical tree and liana species richness from soil and climatic data. *Biodiversity and Conservation*, **4**, 56-90.

Clutton-Brock, , T. H. & Harvey, P. H. 1977. Primate ecology and social organization. *J. Zool. Lond.*, **183**, 1-39.

Clutton-Brock. T. H., Guiness, F. E. & Albon, S. D. 1982. *Red Deer: Behaviour and Ecology of Two Sexes.* Chicago: Chicago University Press.

Collins, D.A. & McGrew, W.C. 1988. Habitats of three groups of chimpanzees *Pan troglodytes* in Western Tanzania compared. *J. Hum. Evol.*, **17**, 553-574.

Coolidge, H. J. 1933. *Pan paniscus* (Pygmy Chimpanzee) from south of the Congo River. *Am. J. Phys. Anthropol.*, **8**, 1-57.

Coppens, Y. East side story: The origin of humankind. *Sci. Am.*, **270**, 88-95.

Cowlishaw, G. C. 1993. *Trade-offs between feeding competition and predation risk in baboons.* Ph.D. Thesis, University College London.

Crockett, C. M. 1987. Howler monkeys: Diet, dimorphism, and demography: perspectives from howlers to hominds. In: The Evolution of Human Behaviour. Primate Models (Ed. by W. G. Kinzey), pp. 115-138. State University of New York Press, New York.

Cronin, J. E. 1983. Apes, humans, and molecular clocks: a reappraisal. In: *New Interpretations of Ape and Human Ancestry*, (Ed. by R. L. Ciochon & R. S. Corruccini), pp, 115-35. New York: Plenum.

Damuth, J. 1981. Population density and body size in mammals. Nature, 290, 699-700.

Damuth, J. & MadFadden, B. J. 1990. Body Size in Mammalian Paleobiology: Estimation and Biological Implications. Cambridge: Cambridge University Press.

Darlington, R. B. 1990. *Regression and Linear Models.* New York: Wiley.

Dasilva, G. L. 1992. The western black- and white colobus as a low-energy strategist: activity budgets, energy expenditure and energy intake. *J. Anim. Ecol.*, **61**, 79-91.

Daubenmire, R. 1978. *Plant Geography: With Special Reference to North America.* Academic Press: New York.

Davenport, M. L., & Nicholson, S. E. 1993. On the relation between rainfall and the Normalized Difference Vegetation Index for diverse vegetation types in East Africa. *Int. J. Remote Sensing,* **14**, 2369-2389.

Demment, M. J. & van Soest, P. J. 1985. A nutritional explanation for body-size patterns of ruminant and non-ruminant herbivores. *Am. Nat.*, **125**, 641-672.

Depew, L. A. 1983. Ecology and behaviour of baboons (*Papio anubis*) at the Shai Hills Game Production Reserve, Ghana. MSc thesis, Cape Coast University, Ghana.

Deshmuhk, I. K. 1984. A common relationship between precipitation and grassland peak biomass for east and southern Africa. *Afr. J. Ecol.*, **22**, 181-186.

Di Fiore, A & Rendall, D. 1994. Evolution of social organisation: A reappraisal for primates by using phylogenetic methods. *Proc. Natl. Acad. Sci. USA.*, **91**, 9941-9945.

Dittus, W. P. J. 1977. The social regulation of populations density and age-sex distribution in the toque monkey. *Behaviour*, **63**, 281-322.

Dittus, W. P. J. 1987. Group fusion among wild toque macaques: an extreme case of inter-group resource competition. *Behaviour*, **100**, 247-291.

Dobson, A.P. & Lyles, A. M. 1989. The population dynamics and conservation of primate populations. *Cons. Biol.*, **3**, 362-380.

Dodd, J. R. & Stanton, R. J. 1990. *Paleoecology: Concepts and Applications.* 2nd Edition. John Wiley & Sons: New York.

Doran, D. 1989. *Chimpanzee and Pygmy Chimpanzee Positional Behavior: The Influence of Environment, Body Size, Morphology, and Ontogeny, on Locomotion and Posture.* Ph.D. Dissertation. State University of New York at Stony Brook, Stony Brook, New York.

Doran, D.M. 1992. Comparison of instantaneous and locomotor bout sampling methods- A case-study of adult male chimpanzee locomotor behaviour and substrate use. *Am. J. Phys. Anthropol.*, **89**, 85-99.

Doran, D. M. 1996. Comparative positional behavior of the African apes. In: *Great Ape Societies* (Ed. by W. C. McGrew, L. F. Marchant & T. Nishida), pp. 213-224. London: Cambridge University Press.

Draper, N. R. & Smith, H. 1981. *Applied regression analysis* (2nd Edition). New York: Wiley.

Dunbar, R. I. M. 1976. Australopithecine diet based on baboon analogy. *J. Hum. Evol.*, **5**, 161-167.

Dunbar, R. I. M. 1983. Theropithecines and hominids: contrasting solutions to the same ecological problem. *J. Hum. Evol.*, **12**, 647-658.

Dunbar, R. I. M. 1984. Reproductive Decisions: An Economic Analysis of gelada baboon Social Strategies. Princeton University Press, Princeton New Jersey.

Dunbar, R. I. M. 1988. *Primate Social Systems.* London: Crom Helm.

Dunbar, R. I. M. 1989. Ecological modelling in an evolutionary context. *Folia. Primtol.*, **53**, 235-246.

Dunbar, R. I. M. 1989. Social systems as optimal strategy sets: the costs and benefits of sociality. In: *Comparative Socioecology* (Ed. by V. Standen & R. Foley), pp. 131-150. Oxford: Blackwell Scientific.

Dunbar, R. I. M. 1990. Environmental determinants of intraspecific variation in body weight in baboons (*Papio* spp.). *J. Zool. Lond.*, **220**, 157-169.

Dunbar, R. I. M. 1991. The functional significance of social grooming in primates. *Folia Primatol.*, **57**, 121-131.

Dunbar, R. I. M. 1992*a*. A model of the gelada socio-ecological system. *Primates*, **33**, 69-83.

Dunbar, R. I. M. 1992*b*. Time: a hidden constraint on the behavioural ecology of baboons. *Behav. Ecol. Sociobiol.*, **31**, 35-49.

Dunbar, R. I. M. 1992*c*. Coevolution of neocortical size, group size and language in humans. *Behav. Ecol. Sociobiol.*, **16**, 681-735.

Dunbar, R. I. M. 1992c. Neocortex size as a constraint on group size in primates. *J. Hum. Evol.*, **20**, 469-493.

Dunbar, R. I. M. 1992d. Behavioural ecology of the extinct papionines. *J. Hum. Evol.*, **22**, 407-421.

Dunbar, R. I. M. 1993*a*. Socioecology of the extinct theropiths: A modelling approach. In: *Theropithecus: The Rise and Fall of a Primate Genus* (Ed. by N. G. Jablonski), pp. 465-485. Cambridge University Press.

Dunbar, R. I. M. 1993*b*. Coevolution of neocortical size, group size and language in humans. Behav. Ecol. Sociobiol., 16, 681-735.

Dunbar, R. I. M. 1994. Ecological constraints on group size in baboons. In*: Animal Societies, Individuals, Interactions and Social Organization* (Ed. by P. Jarman & A. Rossiter), pp. 221-236. Blackwell Scientific Publications, Oxford.

Dunbar, R. I. M. 1995. Neocortex size and group size in primates: a test of the hypothesis. *J. Hum. Evol.*, **28**, 287-296.

Dunbar, R. I. M. 1996. Determinants of group size: A general model. *Proceedings of the British Academy*, **88**, 33-57.

Dunbar, R. I. M. & Dunbar, P. 1988. Maternal time budgets of gelada baboons. *Anim. Behav.*, **36**, 970-980.

Dunbar, R. I. M. & Nathan, M. F. 1972. Social organisation of the Guinea baboon, *Papio papio*, in Senegal. *Folia Primatol.*, **17**, 321-334.

Dunbar, R. I. M. & Sharman, M. 1984. Is social grooming altruistic? *Z. Tierpsychol.*, **64**, 163-173.

Duncan, P. 1980. Time budgets of Camargue horses, II. Time budgets of adult horses and waned sub-adults. *Behaviour*, **72**, 26-49.

Eggeling, W. J. 1947. Observations on the ecology of the Budongo rain forest, Uganda. *J. Ecol.*, **34**, 20-87.

Fedigan, L. & Baxter, M. J. 1984. Sex differences in social organization in free-ranging spider monkeys (*Ateles geoffroyi*). *Primates*, **25**, 279-294.

Feibel, C. S., Harris, J. M. & Brown, F. H. 1991. Palaeoenvironemntal context for the late Neogene of the Turkana Basin. In: *Koobi Fora Research Project, Vol 3* (Ed. by J. M. Harris), pp. 321-370. Oxford: Clarendon Press.

Fleagle, J. G., & Reed, K. E. 1996. Comparing primate communities: a multivariate approach. *J. Hum. Evol.*, **30**, 489-510.

Foley, R. (Ed.) 1984. *Hominid Evolution and Community Ecology: Prehistoric Human Adaptation in Biological Perspective.* London: Academic Press.

Foley, R. 1987. *Another Unique Species: Patterns in Human Evolutionary Ecology.* Longman Scientific and Technical. U.K.

Foley, R. A. 1989. The evolution of hominid social behaviour. In: *Comparative Socioecology: The Behavioural Ecology of Humans and of Other Animals* (Ed. by V. Standen & R. Foley), pp. 473-494. Blackwell Scientific Publications.

Foley, R. A. 1991. Speciation, extinction and climatic change in hominid evolution. *J. Hum. Evol.*, **26**, 275-289.

Foley, R. A. 1992. Evolutionary ecology of fossil hominids. In: *Evolutionary Ecology and Human Behaviour* (Ed. by E. A. Smith & B. Winterhalder), pp. 131-164. New York: Aldine de Gruyter.

Foley, R. A. 1993. The influence of seasonality on hominid evolution. In: *Seasonalithy and Human Ecology* (Ed. by S. J. Ulijaszek & S. S. Strickland), pp. 17-37). Society for the Study of Human Biology Symposium 35.

Foley, R. A. 1996. An evolutionary and chronological framework for human social behaviour. *Proceedings of the British Academy*, **88**, 95-117.

Foley, R. A., & Lee, P. C. 1989. Finite social space, evolutionary pathways, and reconstructing hominid behaviour. *Science*, **243**, 901-906.

Ford, S. M., & Davis, L. C. 1992. Systematics and body size: Implications for feeding adaptations in New World Monkeys. *Am. J. Phys. Anthropol.*, **88**, 415-468.

Frost, P., Medina, E., Menaut, J-C., Solbrig, O., Swift, M. & Walker, B. 1986. Responses of savannas to stress and disturbance. *Biology International (IUBS)*, special issue **10**.

Fruth, B. & Hohmann, G. 1994. Comparative analyses of nest-building behavior in bonobos and chimpanzees. In: *Chimpanze Cultures* (Ed. by R. W. Wrangham, W. C. McGrew, F. B. M. de Waal, & P. G. Heltne), pp. 109-128. Cambridge, MA: Harvard University Press.

Furuichi, T. 1989. Social interactions and the life history of female *Pan pansicus* in Wamba, Zaire. *Int. J. Primatol.*, **10**, 173-197.

Galdikas, B. M. F. 1979. Orang-utan adaptation at Tanjung Putin Reserve: mating and ecology. In: *The Great Apes* (Ed. by D. A. Hamburg & E. R. McCown), pp. 195-234. Benjamin Cummings, Menlo Park: California.

Gentry, A. H. 1982. Neotropical floristic diversity: phytogeographical connections between Central and South America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny? *Ann. Missouri Bot. Gard.*, **69**, 557-593.

Ghiglieri, M. P. 1984. *The chimpanzees of Kibale Forest.* New York: Columbia University Press.

Ghiglieri, M. P. 1986. Feeding ecology and sociality of chimpanzees in Kibale Forest, Uganda. In: *Adaptations to Foraging in Non-Human Primates* (Ed. by P. S. Rodman & J. G. H. Cant), pp. 161-194. New York: Columbia University Press.

Ghiglieri, M. P. 1987. Sociobiology of the great apes and the hominid ancestor. *J. Hum. Evol.*, **16**, 319-357.

Gifford, D. P. 1981. Taphonmy and paleoecology: A critical review of archaeology's sister disciplines. *Adv. Arch. Meth. Theory*, **4**, 365-438.

Gifford-Gonzales, D. 1991. Bones are not enough: analogues, knowledge, and interpretive strategies in zooarchaeology. *J. Anthropological Archaeology*, **10**, 215-254.

Goodall, J. 1968. The behaviour of free-living chimpanzees in the Gombe Stream Reserve. *Anim. Behav. Monogr.*, **1**, 161-311.

Goodall, J. 1986. *The chimpanzees of Gombe: Patterns of behaviour.* Cambridge: Harvard University Press.

Goodman, M., Bailey, W. J., Hayasaka, K., Stanhope, M. J., Slightom, J. & Czelusniak, J. 1994. Molecular evidence on primate phylogeny from DNA sequences. *Am. J. Phys. Anthropol.*, **94**, 3-24.

Gowlett, J. A. J. 1996. The frameworks of early hominid social systems: How many useful parameters of archaeological evidence can we isolate? In: *The Archaeology of Human Ancestry: Power Sex and Tradition* (Ed. by J.Steele & S. Shennan), pp.135-183.

Grant, J. W. A., Chapman, C. A., & Richardson, K. S. 1992. Defended versus undefended home range of carnivores, ungulates and primates. *Behav. Ecol. Sociobiol.*, **31**, 149-161.

Grether, G. F., Palombit, R. A. & Rodman, P. S. 1993. Gibbon foraging decisions and the marginal value model. *Int. J. Primatol.*, **13**, 1-17.

Griffiths, J. F. 1972. *Climates of Africa - World Survey of Climatology*, Volume 10. Amsterdam: Elsevier.

Grine, F. E. 1981. Trophic level differences between "gracile" and "robust" australopithecines: a scanning electron microscope analysis of occlusal events. *S. Afr. J. Sci.*, **77**, 203-230.

Grine, F. & Kay, R. F. 1988. Early hominid diets from quantitative image analysis of dental microwear. *Nature*, **333**, 765-768.

Halperin, S. D. 1979. Temporary association patterns in free rangin chimpanzees: an assessment of individual grouping preferences. In: *The Great Apes* (Ed. by D. A. Hamburg & E. R. McCown), pp. 491-499. Menlo Park, CA: Benjamin/Cummings.

Harding, R. H. & Olsen, D. K. 1986. Patterns of mating among male patas monkeys (*Erythrocebus patas*) in Kenya. *A. J. Primatol.*, **11**, 343-358.

Hartwig-Scherer, S. 1993. Body weight prediction in early fossil hominids: towards a taxon - "independent" approach. Am. J. Phys. Anthropol., 92, 17-36.

Harvey, P. H. & Clutton-Brock, T. H. 1985. Life history variation in primates. *Evolution*, **39**, 559-581.

Harvey, P. H. & Pagel, M. D. 1991. *The Comparative Method in Evolutionary Biology.* Oxford: Oxford University Press.

Hasegawa, M. 1992. Evolution of hominoids as inferred from DNA sequences. In: *Topics in Primatology, Vol I, Human Origins* (Ed. by T. Nishida, W. C. McGrew, P. Marler, M. Pickford & F. B. de Waal), pp. 346-357. Tokoy: Tokyo University Press.

Hoffman, A. A. & Blows, M. W. 1994. Species borders: ecological and evolutionary perspectives. *Trends Evol. Ecol.*, **9**, 223-227.

Hoppe-Dominik, B. 1991. Distribution and status of chimpanzees (*Pan troglodytes verus*) on the Ivory Coast. *Primate Report*, **31**, 45-75.

le Houérou, H. N. 1984. Rain use efficiency: a unifying concept in arid-land ecology. *J. Arid Environment.* **7**, 213-247.

le Houérou, H. N. & Hoste, C. H. 1977. Rangeland production and annual rainfall relations in the Mediterranean basin and in the African Sahelo-Sudanian zone. *J. Range. Mgmt.*, **30**, 181-189.

le Houérou, H. N., & Popov, G. F. 1981. An eco-climatic classification of intertropical Africa (3 maps). *Plant production and Protection Paper.* No. 31. Rome, FAO.

Hounam, C. E., Burgos, J. J., Kalik, M. S., Palmer, W. L., & Rodda, J. 1975. *Drought and Agriculture.* World Meteorological Organization Technical Note 138. WMO **392**: 1-127.

Houston, A. I., McNamara, J. M. & Hutchinson, J. M. C. 1993. General results concerning the trade-off between gaining energy and avoiding predation. *Phil. Trans. R. Soc. Lond. B.*, **341**, 375-397.

Huffman, M. A. 1990. Some socio-behavioral manifestations of old-age. In: *The Chimpanzees of the Mahale Mountains* (Ed. by T. Nishida), pp. 237-255. Tokyo: University of Tokyo Press.

Hulme, M. 1993. CRU0092.DAT. (Version 1.0) constructed and supplied by Dr. Mike Hulme at the Climatic Research Unit, University of East Anglia, Norwich, UK. This work has been supported by the UK Department of the Environment (Contract PECD 7/12/78).

Hunt, K. D. 1989. *Positional Behaviour in Pan troglodytes at the Mahale Mountains and the Gombe Stream National Parks, Tanzania.* Ph. D. thesis.

Huntley, B. J. 1982. Southern African Savannas. In: *Ecology of Tropical Savannas* (Ed. by B. J. Huntley, & B. H. Walker), pp. 101-119. Springer Verlag, New York.

Idani, G., Kuruda, S., Kano, T. & Asato, R. 1994. Flora and vegetation of Wamba forest Central Zaire with reference to bonobo (*Pan paniscus*) foods. *Tropics*, **3**, 309-332.

Isabiyre-Basuta, G. 1988. Free-ranging chimpanzee community in Kibale Forest, Uganda. *Behaviour*, **105**, 135-147.

Isbell, L. 1992. Contest and scramble competition: patterns of female aggression and ranging behaviour among primates. *Behav. Ecol.*, **2**, 143-155.

Isbell, L. A., & Young, T. P. 1996. The evolution of bipedalism in hominids and reduced group size in chimpanzees: alternative responses to decreasing resource availability. J. Hum. Evol., 30, 389-397.

Iwamoto, T., & Dunbar, R. I. M. 1983. Thermoregulation, habitat quality, and the behavioural ecology of gelada baboons. *J. Anim. Ecol.*, **52**, 357-366.

Izawa, K. 1970. Unit groups of chimpanzees and their nomadism in the savanna woodland. *Primates*, **11**, 1-45.

Izawa, K., & Itani, J. 1966. Chimpanzees in Kasakati Basin, Tanganyika. (I) Ecological study in the rainy season 1963-1964. *Kyoto Univ. Afr. Stud.*, **1**, 73-156.

James, F. C. & McCulloch, C. E. 1985. Data analysis and the design of experiments in ornithology. In: *Current Ornithology Vol. 2.* (Ed. by R. F. Johnston), pp. 1-63. New York: Plenum.

James, F. C. & McCulloch, C. E. 1990. Multivariate analysis in ecology and systematics: Panacea or Panora's Box? *Ann. Rev. Ecol. Syst.*, **21**, 129-166.

Janis, C. 1976. The evolutionary strategy of the equidae and the origins of rumen and caecal digestion. *Evolution*, **30**, 757-774.

Janson, C. H. & Goldsmith, M. L. 1995. Predicting group size in primates: foraging costs and predation risks. *Behavioural Ecology*, **6**, 326-336.

Jarman, P.J. & Jarman, M. 1973. Daily activity of impala. *East. Afr. Wildl. J.*, **11**, 75-92.

Jolly, A. 1972. *The Evolution of Primate Behaviour*. McMillan: New York.

Jones, C. & Sabater-Pi, J. 1971. Comparative ecology of *Gorilla gorilla* (Savage and Wyman) and *Pan troglodytes* (Bluemenbach) in Rio Muni, West Africa. *Bibliotheca Priomatologica*, **13**, 1-96.

Jungers, W. L. & Susman, R. L. 1984. Body size and skeletal allometry in African apes. In: *The Pygmy Chimpanzee* (Ed. by R. L. Susman), pp. 131-177. New York: Plenum Press.

Kano, T. 1971. Distribution and adaptation of the chimpanzee in the open country on the eastern shore of Lake Tanganyika. *Kyoto Univ. Afr. Stud.*, **7**, 37-129.

Kano, T. 1972. Distribution and Adaptation of the chimpanzees on the Eastern Shore of lake Tanganiyika. *Kyoto Univ. Afr. Stud.*, **7**, 37-129.

Kano, T. 1980. Social behaviour of wild pygmy chimpanzees (*Pan paniscus*) of Wamba: A preliminary report. *J. Hum. Evol.*, **9**, 243-260.

Kano, T. 1983. An ecological study of the pygmy chimpanzee (*Pan paniscus*) of Yalosidi, Republic of Zaire. *Int. J. Primatol.* **4**, 1-31.

Kano, T. 1984. Distribution of pygmy chimpanzees (*Pan paniscus*) in the Central Zaire Basin. *Folia Primatol.*, **43**, 36-52.

Kano, T. 1992. *The Last Ape: Pygmy Chimpanzee Behaviour and Ecology*. Stanford, CA: Stanford University Press.

Kano, T., & Mulavwa, M. 1984. Feeding Ecology of *Pan paniscus* at Wamba. In: *The Pygmy Chimpanzee: Evolutionary Biology and Behaviour* (Ed. by R.L. Susman), pp. 233-274. New York: Plenum Press.

Kappelman, J. 1984. Plio-Pleistocene environments of Bed I and lower Bed II, Olduvai Gorge, Tanzania. *Palaeogeogr., Palaeoclimat., Palaeoecol.* **48**, 171-196.

Kawabe, M. 1966. One observed case of hunting behavior among wild chimpanzees living in the savanna woodland of western Tanzania. *Primates*, **7**, 393-396.

Kawamuto, Y., Shotake, T. & Nozawa, K. 1982. Genetic differentiation among three genera of Family Cercopithecidae. *Primates*, **23**, 272-286.

Kay, R. F. 1975. The functional adapatations of primate molar teeth. *Am. J. Phys. Anthropol.*, **43**, 195-216.

Kay, R. F. 1984. On the use of anatomical features to infer foraging behavior in extinct primates. In: *Adaptations for Foraging in Nonhuman Primates* (Ed. by P. S. Rodman & J. G. H. Cant), pp. 21-53. New York: Colombia University Press.

Kay, R. F., & Covert, B. 1984. Anatomy and behaviour of extinct primates. In: Food Acquisition and Processing in Primates (Ed by D. Chivers, B. Wood & A. Bilsborough), pp. 467-508.

Kay, R. F., & Simons, E. L. 1980. The ecology of Oligocene African Anthropoidea. Int. J. Primatol., 1, 21-37.

Keay, R. W. J. 1959. *Vegetation Map of Africa, South of the Tropic of Cancer.* Oxford University Press, Oxford.

Kelley, J. 1993. Taxonomic implications of sexual dimorphism in *Lufengpithecus.* In: *Species, Species Concepts, and Primate Evolution* (Ed. by W. H. Kimbel & L. B. Martin), pp. 429-58. New York: Plenum.

Kenyatta, C. G. 1995. *Ecological and Social Constraints on Maternal Investment Patterns.* Ph.D. University College London.

Kerr, J. T. & Packer, L. 1997. Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature*, **385**, 252-254.

Kiester, A. R. & Slatkin, M. A. 1974. A strategy of movement and resource utilisation. *Theor. Pop. Biol.*, **6**, 1-20.

Kimbel, W. H., Johanson, d. C. & Rak, Y. 1994. The first skull and other new discoveries of *Australopithecus afarensis* at Hadar, Ethiopia. *Nature*, **368**, 449-51.

Kingston, J. D., Marino, B. D., & Hill, A. 1994. Isotopic evidence for neogene hominid paleoenvironments in the Kenya rift valley. Science, 264, 955-959.

Kinzey, W. G. 1984. The dentition of the pygmy chimpanzee, *Pan paniscus.* In: *The Pygmy Chimpanzee* (Ed. by R. L. Susman), pp. 65-88. London: Academic Press.

Kinzey, W. G. (Ed). 1987. The Evolution of Human Behaviour: Primate Models. State University of New York, New York.

Kleiber, M. 1961. *The Fire of Life.* Wiley: New York.

Kortlandt, A. 1983*a*. Rainfall data for some chimpanzee sites in Africa (Climatology for primatologists). (Available on request).

Kortlandt. A. 1983*b*. Marginal Habitats of Chimpanzees. *J. Hum. Evol.*, **12**, 213-278.

Kortlandt, A. 1984. Habitat richness, foraging range and diet in chimpanzees and some other primates. In: *Food Acquisition and Processing in Primates* (Ed. by D. A. Chivers, B. A. Wood & A. Bilsborough), pp. 119-159. New York: Plenum.

Krebs, J. & Davies, N. B. 1984. Behavioural Ecology. Second Edition. Oxford: Blackwell.

Kuroda, S. 1979. Grouping of the pygmy chimpanzees. *Primates*, **20**, 161-183.

Kuroda, S. 1980. Social Behaviour of the Pygmy Chimpanzees. *Primates*, **21**, 181-197.

Kuruda, S., Nishihara, T., Suzuki, S. & Oko, R. A. 1996. Sympatric chimpanzees and gorillas in the Ndoki Fores, Congo. In: *Great Ape Societies* (Ed. by W. C. McGrew, L. F. Marchant & T. Nishida), pp.71-81. Cambridge: Cambridge University Press.

Laporte, L. F. & Zihlman, A. L. 1983. Plates, climate and hominoid evolution. *South African Journal of Science*, **79**, 96-100.

Lawrence, D. 1971. The nature and essence of paleoecology. *J. Paleontology*, **45**, 593-607.

Leakey, M. G., Feibel, C. S., McDougall, & Walker, A. 1995. New four-million-year-old hominid species from kanapoi and Allia Bay, Kenya. *Nature*, **376**, 565-571.

Lee, P. C. 1989. Comparative ethological approaches in modelling hominid behaviour. *OSSA: International Journal of Skeletal Research*, **14**, 113-126.

Lee, P. C. 1991. Adaptations to environmental change: an evolutionary perspective. In: *Primate Responses to Environmental Change* (Ed. by H. O. Box), pp. 39-56. London: Chapman & Hall.

Lee, P. C., & Foley, R. A. 1993. Ecological energetics and extinction of giant gelada baboons. In: *Theropithecus: The Rise and Fall of a Primate Genus* (Ed. by N. G. Jablonski), pp.

Leighton, M. 1993. Modelling dietary selectivity by bornean orangutans: evidence for integration of mulitple criteria in fruit selection. *Int. J. Primatol.*, **14**, 257-313.

Leith, H. & Box, E. O. 1972. Evapotranspiration and primary production: C. W. Thornthwaite memorial model. *Publ. Climatol.*, **25**, 37-46.

Lewis, C. (Ed.). 1975. *New Oxford Atlas*. London: Oxford University Press.

Lincare, E. 1992. *Climate Data and Resources*. London: Routledge.

Lowen, C. & Dunbar, R. I. M. 1994. Territory size and defendability in primates. *Behav. Ecol. Sociobiol.*, **35**, 347-354.

MacArthur, R. H. & Wilson, E. O. 1967. *The Theory of Island Biogeography*. Princeton, N.J: Princeton University Press.

Magurran, A. E. 1988. *Ecological Diversity and its Measurement*. Princeton University Press, Princeton.

Malenky, R. K. 1990. *Ecological factors affecting food choice and social organization in Pan paniscus*. Ph.D. Thesis, SUNY at Stony Brook, Stony Brook, New York.

Malenky, R. K. & Wrangham, R. W. 1994. A quantitative comparison of terrestrial herbaceous food consumption by *Pan paniscus* in the Lomako Forest, Zaïre, and *Pan troglodytes* in the Kibale Forest, Uganda. *Am. J. Primatol.*, **32**, 1-12.

Malenky, R.K., & Stiles, E.W. 1991. Distribution of terrestrial herbaceous vegetation and its consumption by *Pan paniscus* in the Lomako forest, Zaire. *Am. J. Primatol.*, **23**, 153-169.

Mangel, M. & Clark, C. W. 1986. Towards a unified foraging theory. *Ecology*, **67**, 1127-1138.

Manly, B. F. J. 1991. *Randomization and Monte Carlo Methods in Biology*. London: Chapman & Hall.

Marean, C. W. 1989. Sabertooth cats and thier relevance for early hominid diet and evolution. J. Hum. Evol., 18, 559-582.

Markham, C. G. 1970. Seasonality of precipitation in the United States. *Assoc. American Geographers Annals*. **60**, 593-597.

Marriot (1988) (from one of the Japanese time budget papers / Watts).

Marsh, C. W. 1981. Time budget of Tana River Red Colobus. *Folia Primatol.*, **35**, 30-50.

Martin, R. D. 1983. *Human Brain Evolution in an Evolutionary Context.* New York: American Museum of Natural History.

Maryanski, A. R. 1996. African ape social networks: a blueprint for reconstructnig early hominid social structure. In: *The Archaeology of Human Ancestry: Power, Sex and Tradition* (Ed. by J. Steele & S. Shennan), pp. 67-90. London: Routledge.

McBeath, N.M., & McGrew, W.C. 1982. Tools used by wild chimpanzees to obtain termites at Mt. Assirik, Senegal: The influence of habitat. *J. Hum. Evol.*, **11**, 65-72.

McFarland, D. 1974. Time-sharing as a behavioural phenomenon. *Adv. Stud. Behav.*, **5**, 201-225.

McFarland, D. & Houston, A. I. 1981. *Quantitative Ethology: The State Space Approach.* London: Pitman.

McFarland-Symington, M. 1988. food competition and foraging party size in the black spider monkey (*Ateles paniscus chantek*). *Behaviour*, **105**, 117-134.

McGrew, W. C. 1981. The female chimapnzee as a female evolutionary prototype. In: *Woman the Gatherer* (Ed. by F. Dahlberg), pp. 35-73. New Haven, CT: Yale University Press.

McGrew, W. C. 1983. Animal foods in the diets of wild chimpanzees (*Pan troglodytes*): why cross-cultural variation? *J. Ethol.*, **1**, 46-61.

McGrew, W. C. 1992. *Chimpanzee Material Culture: Implications for Human Evolution.* Cambridge: Cambridge University Press.

McGrew, W. C., Baldwin, P. J. & Tutin, C. E. G. 1983. A reply to Kortlandt's "Marginal Habitats of Chimpanzees". *J. Hum. Evol.*, **12**, 413-417.

McGrew, W.C., Baldwin, P.J., & Tutin, C.E.G. 1981. Chimpanzees in a Hot, Dry and Open Habitat: Mt. Assirik, Senegal, West Africa. *J. Hum. Evol.*, **10**, 227-244.

McGrew, W.C., Baldwin, P.J., & Tutin, C.E.G. 1988. Diet of Wild Chimpanzees (*Pan troglodytes*) at Mt. Assirik, Senegal: I. Composition. *Am. J. Primatol.*, **16**, 213-226.

McHenry, H. M. 1992. Body size and proportions in early hominids. *Am. J. Phys. Anthropol.*, **87**, 407-431.

McHenry, H. M. 1994. Behavioural ecological implications of early hominid body size. *J. Hum. Evol.*, **27**, 77-87.

McNaughton, S. J. 1985. Ecology of a grazin ecosystem: the Serengeti. *Ecol. Monogr.*, **55**, 259-294.

Melnick, D. J. & Pearl, M. C. 1987. Cercopithecines in multimale groups: genetic diversity and population structure. In: *Primate Societies* (Ed. by B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker), pp. 121-134. Chicago: University of Chicago Press.

Miller, A. A. 1953. *Climatology.* 8th Edition. London: Methuen.

Mitani, J. C. & Nishida, T. 1993. Contexts and social correlates of long-distance calling by male chimpanzees. *Anim. Behav.*, **45**, 735-746.

Mitani, J. C. & Rodman, P. 1979. Territoriality: the relation of ranging pattern and home range size to defendability, with an analysis of territoriality among primate species. *Behav. Ecol. Sociobiol.*, **5**, 241-251.

Mohr, E. C. J., van Baren, F. A. & van Schuylenborgh, J. 1972. *Tropical Soils.* 3rd Edition. The Hague: Mouton-Ichtair Baru-van Hoeve.

Moore, J. 1992. Savanna Chimpanzees. In: *Topics in Primatology. Vol. I : Human Origins* (Ed. by T. Nishida, W. C. McGrew, P. Marler, M. Pickford & F. B. W. de Waal), pp. 99-118. Tokyo: Tokyo University Press.

Moore, J. 1994. Plants of the Tongwe East Forest Reserve (Ugalla) Tanzania. *Tropics*, **3**, 333-340.

Moore, J. 1996. Savanna chimpanzees, referential models and the last common ancestor. In: *Great Ape Societies* (Ed. by W. C. McGrew, L. F. Marchant & T. Nishida), pp. 275-292. London: Cambridge University Press.

Morbeck, M. E. & Zihlman, A. L. 1989. Body size and proportions in chimpanzees, with special reference to *Pan troglodytes schweinfurthii* from Gombe National Park, Tanzania. *Primates*, **30**, 369-382.

Morell, V. 1994. Will primate genetics split one gorilla into two? *Science*, **265**, 1661.

Morin, P. A., Moore, J., Chakraborty, R., Jin, L., Goodall, J., & Woodruff, D. S. 1994. Kin selection, social structure, gene flow and, and the evolution of chimpanzees. *Science,* **265**, 1193-1201.

Mount, L. E. 1979. *Adaptation to Thermal Environment.* London: Arnold.

Moutsamboute, J. -M., Yumoto, T., Mitani, M., Nishihara, T., Suzuki, S & Kuruda, S. 1994. Vegetation and list of plant species identified in the Nouabale-Ndoki Forest, Congo. *Tropics*, **3**, 227-293.

Nakagawa, N. 1989. Feeding strategies of Japanese monkeys against deterioration of habitat quality. *Primates*, **30**, 1-16.

Newton, P. H. 1992. Feeding and ranging patterns of forest hanuman langurs (*Presbytis entellus*). *Int. J. Primatol.*, **13**, 245-286.

Nicholson, S. E., Kim, J. & Hoopingarner, H. 1988. *Atlas of African Rainfall and Its Interannual Variability.* Department of Meteorology, Florida State University of Tallahassee, Florida 32306.

Nishida, T. 1968. The social group of wild chimpanzees in the Mahale Mountains. *Primates*, **9**, 167-224.

Nishida, T., Wrangham, R.W., Goodall, J., & Uehara, S. 1983. Local differences in plant-feeding habits of chimpanzees between the Mahale Mountains, and Gombe National Park, Tanzania. *J. Hum. Evol.*,**12**, 467-480.

Nishida, T. (Ed.). 1990. *The Chimpanzees of the Mahale Mountains: Sexual and Life History Strategies.* Tokyo: University of Tokyo Press.

Nishida, T. & Hiraiwa-Hasegawa, M. 1987. Chimpanzees and bonobos: cooperative relationships among males. In: *Primate Societies* (Ed. by B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker), pp. 165-180. Chicago: University of Chicago Press.

Nishida, T., & Tachibana, T. 1987. Primatology Report Number 7. *Anima*, **173**, 98-104 [in Japanese]. (Cited in Sugiyama, 1988).

Noy-Meir, I. 1985. Desert ecosystem structure and function. In: *Hot Desert and Arid Shrublands. Ecosystems of the World.* **12**, 83-103.

O'Brien, E. M. 1988. Climatic correlates of species richness for woody "edible" plants across southern Africa. *Monogr. Syst. Bot. Missouri Bot. Gard.*, **25**, 385-401.

Oliver, J. S., Sikes, N. E., & Stewart, K. M. (Eds). 1994. *Early Hominid Behavioural Ecology.* Academic Press, London.

Pastor-Nieto, R & Williamson, D. K. (*in review*). The effect of seasonality on the geographical distribution of Neotropical primates. *J. Tropical Ecology.*

Peet, R. K. 1974. The measurement of species diversity. *Ann. Rev. Ecol. Syst.*, **5**, 285-307.

Peters, C. R. 1987. Nut-like oil seeds: food for monkeys, chimpanzees, humans, and probably ape-men. *Am. J. Phys. Anthropol.*, **73**, 333-363.

Peters, C. R. & O'Brien, E. M. 1981. The early hominid plant-food niche: insights from an analysis of plant exploitation by *Homo*, *Pan*, and *Papio* in eastern and southern Africa. *Curr. Anthropol.*, **22**, 127-140.

Peters, C. R. & Blumenschine, R. J. 1995. Landscape perspectives on possible land use patterns for Early Pleistocene hominids in the Olduvai Basin, Tanzania. *J. Hum. Evol.*, **29**, 321-362.

Peters, C. R. & Maguire, B. 1981. Wild plant foods of the Makapansgat area: A modern ecosystems analogy for *Australopithecus africanus* adaptations. *J. Hum. Evol.*, **10**, 565-583.

Peters, C. R., O'Brien, E. M. & Box, E. O. 1984. Plant types and seasonality of wild-plant foods, Tanzania to south-western Africa: resources for models of the natural environment. *J. Hum. Evol.*, **13**, 397-414.

Peters, R. H. 1983. *The Ecological Implications of Body Size.* Cambridge: Cambridge University Press.

Pianka, E. R. 1978. *Evolutionary Ecology.* John Wiley & Sons: New York.

Pickford, M. 1991. Growth of the Ruwenzoris and their impact on palaeoanthropology. In: *Primatology Today* (Ed. by A. I. Ehara, T. Kimura, O. Takenada & M. Iwamoto), pp. 55513-516. Elsevier Science Publications: Amsterdam.

Picq, P. 1993. Un essai de reconstitution de la socioécologie d'Australopithecus afarensis (An attempted reconstruction of the socioecology of Australopithecus afarensis. *C. R. Acad. Sci. Paris*, t.**317**, Série II, 1357-1362.

Plummer, T. W. & Bishop, L. C. 1994. Hominid palaeoecology at Olduvai Gorge, Tanzania as indicated by antelope remains. *J. Hum. Evol.*, **27**, 47-75.

Porter, A. M. W. 1993. Sweat and thermoregulation in hominids. Comments prompted by the publications of P.E. Wheeler 1984-1993. J. Hum. Evol., 25, 417-423.

Post, D. 1981. Activity patterns of yellow baboons (*Papio cynocephalus*) in the Amboseli National Park, Kenya. *Anim. Behav.*, **29**, 357-374.

Potts, R. 1994. Variables versus models of early pleistocene hominid land use. *J. Hum. Evol.*, **27**, 7-24.

Potts, R. 1987. Reconstruction of early hominid socioecology: A critique of primate models. In: *The Evolution of Human Behaviour: Primate Models.* (Ed. by W. G. Kinzey), pp. 28-50. State University of New York Press, New York.

Poulin, B., Lefebvre, G., McNeil, R. 1992. Tropical avian phenology in relation to abundance and exploitation of food resources. *Ecology*, **73**, 2295-2309.

Prentice, M. L. & Denton, G. H. 1988. In: *Evolutionary History of the Robust Australopithecines* (Ed by F. E. Grine), pp. 383-403. Aldine de Gruyter: New York.

Prost, J. H. 1985. Chimpanzee behavior and models of hominization. In: *Primate Morphophysiology, Locomotor Analyses and Human Bipedalism.* (Ed. by S. Kondo), pp. 289-303. Tokyo: University of Tokyo Press.

Pusey, A. E. 1978. *The physical and social development of wild adolescent chimpanzees (Pan troglodytes schweinfurthii).* Ph.D. dissertation, Stanford University.

Rasmussen, D. R. 1983. Correlates of patterns of range use of a troop of yellow baboons (*Papio cynocephalus*). II. Spatial structure, cover density, food gathering, and individual behaviour patterns. *Anim. Behav.*, **31**, 834-856.

Rayner, R. J., Moon, B. P., & Masters, J. C. 1993. The makapansgat australopithecine environment. *J. Hum. Evol.*, **24**, 219-231.

Reed, K. E. 1997. Early hominid evolution and ecological change through the African Plio-Pleistocene. *J. Hum. Evol.*, **32**, 289-322.

Rendall, D., & DiFiore, A. 1995. The road less travelled: Phylogenetic perspectives in primatology. Evol. Anthropol. ? 43-52.

Reynolds, P. C. 1976. The emergence of early hominid social organizations: I. The attachement systems. *Yrbk. Phys. Anthropol.*, **20**, 73-95.

Reynolds, V., & Reynolds, F. 1965. Chimpanzees of the Budongo Forest. In: *Primate Behaviour.* (Ed. by I. DeVore), pp. 368-424. New York: Holt, Reinhart & Winston.

Robinson, J. G. 1986. Seasonal variation in the use of time and space by the wedge-capped capuchin monkey, *Cebus ouvaceus*: implications for foraging theory. *Smithsonian Contributions to Zoology*, **341**, 1-60.

Rodman, P. S. 1996. Virtual monkeys feed efficiently in large groups on small uniformly dispersed patches: more results of simulations examining group size and foraging efficiency. *Am. J. Phys. Anthropol.*, **S22**, 201.

Rodman, P. S. & McHenry, H. 1980. Bioenergetics and the origin of hominid bipedalism. *Am. J. Phys. Anthropol.*, **52**, 103-106.

Rodseth, L., Wrangham, R. W., Harrigan, A. M., & Smuts, B. B. 1991. The human community as a primate society. *Curr. Anthropol.*, **32**, 221-254.

Rose, L., & Marshall, F. 1996. Meat-eating, hominid sociality and home-bases revisted. *Curr. Anthropol.*, **37**, 307-338.

Rose, M. D. 1991. The process of bipedalization in hominds. In: *Origine(s) de la Bipedie chez les Hominides* (Ed. B. Senut & Y. Coppens), pp. 37-48. Cahirs de Palaeoanthropologie. Paris: Editions du Centre National de la Recherche Scientifique.

Rosenzweig, M. L. 1968. Net Primary Productivty of terrestrial communities: Prediction from climatological data. *Am. Nat.*, **102**, 67-74.

le Roux, X., Bariac, T. & Mariotti, A. 1995. Spatial partitioning of the soil water resource between grass and shtrub components in a West African humid savanna. *Oecololgia*, **104**, 147-155.

Rowell, T. W. 1994. Reification of social systems. *Evol. Anthropol.*, **2**, 135-137.

Rubenstein, D I. & Wrangham, R. W. 1986. *Ecological Aspects of Social Evolution: Birds and Mammals.*

Ruff, C. B. 1991. Climate and body shape in hominid evolution. *J. Hum. Evol.*, **21**, 81-105.

Rugg, D. J. & Buech, R. R. 1990. Analysing time budgets with markov chains. *Biometrics*, **46**, 1123-1131.

Rutherford, M. C. 1980. Annual plant production-precipitation relations in arid and semi-arid regions. *S. Afr. J. Sci.*, **76**, 53-56.

Rutherford, M. C. & Westfall, R. H. 1994. *Biomes of Southern Africa: An Objective Categorization.* Memoires of the Botanical Survey of Southern Africa, No. 63.

Ruvulo, M., Pan, D., Zehr, S., Goldberg, T., Disotell, T., & von Dornum, M. 1994. Gene trees and hominoid phylogeny. *Proceedings of the National Academy of Sciences, U.S.A.*, **91**, 8900-8904.

Ryan, A. S. & Johanson, D. C. 1989. Anterior dental microwear in Australopithecus afarensis: comparisons with human and nonhuman primates. *J. Hum. Evol.*, **18**, 235-268.

Rylands, A. B. 1995. A species list for the new world primates (Platyrrhini): distribution by country, endemism, and conservation status according to the mace-land system. *Neotropical Primates*, **3(suppl.)**, 113-164.

Sabater-Pi, J. 1979. Feeding behaviour and diet of chimpanzees (*Pan troglodytes*) in the Okorobikó Mountains of Rio Muni (West Africa. *Z. Tierpsychol.*, **50**, 265-281.

van Schaik, C. P. 1983. Why are diurnal primates living in groups? *Behaviour*, **87**, 12-144.

van Schaik, C. P. & van Hoof, J. 1983. On the ultimate causes of primate social systems. *Behaviour*, **85**, 91-117.

van Schaik, C. P. & van Hooff, J. A. R. A. M. 1996. Toward an understanding of the orangutan's social system. In: *Great Ape Societies* (Ed. by W. C. McGrew, L. F. Marchant & T. Nishida), pp. 3-15. Cambridge: Cambridge University Press.

van Schaik, C. P. & van Noordwijk, M. A. 1986. The hidden costs of sociality: intra-group variation in feeding strategies in Sumatran long-tailed macaques (*Macaca fascicularis*). *J. Zool. Lond.*, **206**, 533-549.

van Schaik, C. P., van Noordwijk, M.A., DeBoer, R. J. & Den Tonkelaar, I. 1983. The effects of group size on time budgets and social behaviour in wild long-tailed macaques. *Behav. Ecol. Sociobiol.*, **13**, 173-181.

van Schaik, C. P., Terborgh, J. W. & Wright, S. J. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Ann. Rev. Ecol. System.*, **24**, 353-377.

Schaller, G. B., & Lowther, G. R. 1969. The relevance of carnivore behavior to the study of early hominids. *Southwestern Journal of Anthropology*, **25**, 307-341.

Schaller, G. H., Hu, J., Pan, W. & Zhu, J. 1985. *The Giant Pandas of Woolong.* Chicago: University of Chicago Press.

Schmidt, H. 1928. Der jährliche Gang der Niederschläge in Afrika. *Arch. dt. Seewarte.* **46**, 1-45. (cited in Tuhkanen 1980).

Sear, R. 1994. *A Quantitative Analysis of Gibbon Behavioural Ecology.* MSc Thesis, University College London.

Sept, J. 1992. Archaeological evidence and ecological perspectives for reconstructing early hominid subsistence behavior. In: *Advances in Archaeological Method and Theory* (Ed. by M. B. Schiffer), pp. 1-56. Tucson: University of Arizona Press.

Shea, B. T. 1990. Dynamic morphology: growth, life history, and ecology in primate evolution. In: *Primate Life History and Evolution* (Ed. by C. J. DeRousseau), pp. 325-352. New York: Wiley-Liss.

Shea, B. T., Leigh, S. R., & Groves, C. P. 1993. Multivariate craniometric variation in chimpanzees: implications for species identification in paleoanthropology. In: *Species, Species Concepts, and Primate Evolution* (Ed. by W. H. Kimbel & L. B. Martin), pp. 265-296. New York: Plenum.

Shipman, P & Harris, J. M. 1988. Habitat preference and paleoecology of *Autralopithecus boisei* in Eastern Africa. In: *Evolutionary History of the 'Robust' Australopithecines* (Ed. by F. E. Grine), pp. 383-403. Aldine: New York.

Sigg, H. & Stolba, A. 1981. Home range and daily march in a hamadryas baboon troop. *Folia Primatol.*, **36**, 40-75.

Sikes, N. E. 1994. Early hominid habitat preferences in East Africa: Paleosol carbon isotopic evidence. *J. Hum. Evol.*, **27**, 25-45.

Sikes, N. E. & Wood, B. A. 1996. Early hominid evolution in Africa: the search for ecological focus. *Evol. Anthropol.* **4**, 155-159.

Slatkin, M. & Hausfater, G. 1976. A note on the activity patterns of a solitary male baboon. *Primates*, **17**, 311-322.

Smuts, B.B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W. & Struhsaker, T. T. (Eds). 1987. *Primate Societies.* Chicago: University of Chicago Press.

van Soest, P. J. 1982. *The Nutritional Ecology of the Ruminant.* Cornell University Press: Ithaca.

Sokal, R. R., & Rohlf, F. J. 1984. *Biometry.* W. H. Freeman: San Francisco.

Southgate, D. A. T. 1991. Nature and variability of human food consumption. *Phil. Trans. R. Soc. B*, **334**, 281-288.

Southwick, C., Zhang, Y., Jiang, H., Qu, W. 1991. Comparative ecology of rhesus populations at latitudinal extremes in China. In: *Primatology Today* (Ed. by A. Ehara, T. Kimura, O. Takenaka, M. Iwamoto), pp. 25-28. Amsterdam: Elsevier Science Publications.

Spinage, C. L. 1968. A quantitative study of the daily activity of waterbuck. *East. Afr. Wildl. J.*, **6**, 89-93.

Stacey, P. 1986. Group size and foraging efficiency in yellow baboons. *Behav. Ecol. Sociobiol.*, **18**, 175-187.

Stanley, S. M. 1992. An ecological theory for the origin of *Homo. Paleobio.*, **18**, 237-257.

Steele, J. 1996. On predicting hominid group sizes. In: The Archaeology of Human Ancestry: Sex, Power and Tradition (Ed. by J. Steele & S. Shennan), pp. 230-252.

Stelzner, J. K. 1988. Thermal effects on movement patterns of yellow baboons. *Primates*, **29**, 91-105.

Stern, N. 1993. The structure of the lower Pleistocene arhcaoelogicla record: A case study from the Koobi Fora Formation. *Curr. Anthropol.*, **34**, 201-255.

Stern, N. 1994. The implications of time-averaging for reconstructing the land-use patterns of early tool-using hominids. *J. Hum. Evol.*, **27**, 89-106.

Stoltz, L & Saayman, G. S. 1970. Ecology and behaviour of baboons in the Transvaal. *Ann. Transvaal Mus.*, **26**, 99-143.

Strier, K. B. 1994. Myth of the typical primate. *YrBk. Phsy. Anthropol.*, **37**, 233-271.

Strivastava, A. & Dunbar, R. I. M. 1996. The mating system of Hanuman langurs: a problem in optimal foraging. *Behav. Ecol. Sociobiol.*, **39**, 219-226.

Strum, S. C., & Mitchell, W. 1987. Baboon models and muddles. In: The Evolution of Human Behaviour: Primate Models. (Ed. by W. G. Kinzey), pp. 87-104. State University of New York Press, New York.

Sugiyama, Y. 1968. Social organization of chimpanzees in the Budongo Forest, Uganda. *Primates*, **9**, 225-258.

Sugiyama, Y. 1981. Observations on the population dynamics and behaviour of wild chimpanzees at Bossou, Guinea. 1979-1980. *Primates*, **22**, 435-444.

Sugiyama, Y. 1984. Population dynamics of wild chimpanzees at Bossou, Guinea, between 1976 and 1983. *Primates*, **25**, 391-400.

Sugiyama, Y. 1994. Age-specific birth-rate and lifetime reproductive success of chimpanzees at Bossou, Guinea. *Am. J. Primatol.*, **32**, 311-318.

Sugiyama, Y., & Koman, J. 1979. Social structure and dynamics of wild chimpanzees at Bossou, Guinea. *Primates.*, **20**, 323-339.

Sugiyama, Y. & Koman, J. 1987. A preliminary list of chimpanzee's alimentation at Bossou, Guinea. *Primates*, **28**, 133-147.

Susman, R. L. 1987. Chimpanzees: pygmy chimpanzees and common chimpanzees: models for the behavioral ecology of the earliest hominids. In: *The Evolution of Human Behaviour. Primate Models* (Ed. by W. G. Kinzey), pp. 51-71. State University of New York Press, New York.

Susman, R. L., Stern Jr, J. T. & Jungers, W. L. 1985. Locomotor adaptations in the Hadar hominids. In: *Ancestors: the Hard Evidence* (Ed. by E. Delson), pp. 184-192. New York: Alan R. Liss.

Suzuki, A. 1966. On the insect-eating habits among wild chimpanzees living in the savanna woodland of Western Tanzania. *Primates*, **7**, 481-487.

Suzuki, A. 1969. An ecological study of chimpanzees in a savanna woodland. *Primates*, **10**, 103-148.

Suzuki, A. 1971. Carnivory and cannibalism observed among forest-living chimpanzees. *J. Anthrop., Soc. Nippon.*, **79**, 30-48.

Szalay, F. E. & Delson, E. 1979. *The Evolutionary History of the Primates.* New York: Academic Press.

Tabachnik, B. G & Fidell, S. 1989. *Using Multivariate Statistics, 2nd Edition.* New York: Harper Collins Publishers.

Takasaki, H., Nishida, T., Uehara, S., Norikoshi, K., Kawanaka, K., Takahata, Y., Hiraiwa-Hasegawa, M., Hasegawa, T., Hayaki, H., Masui, K., Huffman, M.A. 1990. Summary of Meteorological Data at Mahale Research Camps, 1973-1988. In: *The chimpanzees of the Mahale Mountains: Sexual and life-history strategies.* (Ed. by T. Nishida), pp. Tokyo: University of Tokyo Press.

Takayoshi, T. Kano, T. & Mulavwa, M. 1984. Feeding Competition of the Pygmy Chimpanzee. In: *The Pygmy Chimpanzee.* (Ed. by R. L. Susman), pp. 131-177. New York: Plenum Press.

Tanner, N. M. 1981. On Becoming Human: A Model of Transition from Ape to Human an the Reconstruction of Early Human Social Life. London: Cambridge University Press.

Tanner, N. M. 1987. Gathering by femals: the chimpanzee model revisited and the gathering hypothesis. In: The Evolution of Human Behaviour. Primate Models (Ed. by W. G. Kinzey), pp. 3-27 State University of New York Press, New York.

Taylor, C. R., Heglund, N. C., & Maloiy, G. M. O. 1982. Energetics and mechanics of terrestrial locmotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *J. Exptl. Biol.*, **97**, 1-21.

Taylor, C. R., Norman, C. H., McHahon, T. A., & Looney, T. R. 1980. Energetic cost of generating muscular force during running. J. Exptl. Biol., 86, 9-18.

Teleki, G. 1977. *Spatial and temporal dimensions of routine activities by chimpanzees in Gombe National Park, Tanzania: an ethological study of adaptive strategy.* Ph.D. dissertation, Pennsylvania State University.

Teleki, G. 1981. The omnivorous diet and eclectic feeding habits of chimpanzees in Gombe National Park, Tanzania. In: *Omnivorous Primates: Gathering and Hunting in Human Evolution.* (Ed. by R. S. O. Harding & G. Teleki), pp. 303-343. Columbia University Press, New York.

Terborgh, J. 1983. *Five New World Primates.* Princeton Univ. Press.

Terborgh, J., & Janson, C. H. 1986. The socio-ecology of primate groups. *Ann. Rev. Ecol. Syst.*, **17**, 111-135.

Thompson-Handler, N., Malenky, R. & Reinartz, G. (Eds). 1995. *Action plan for Pan paniscus: Report on free-ranging populations and proposals for their preservation.* Milwaukee, Wisconsin: Zoological Society of Milwaukee County.

Thompson-Handler, N., Malenky, R. K. & Badrian, N. 1984. Sexual behavior of *Pan paniscus* under natural conditions in the Lomako Forest, Equateur, Zaïre. In: *The Pygmy Chimpanzee: Evolutionary Biology and Behavior* (Ed. by R. L. Susman), pp. 347-368. New York: Plenum Press.

Thompson-Handler, N., Malenky, R. K. & Reinartz, G. E. (Eds.). 1995. *Action Plan for Pan paniscus: Report on free-ranging population and proposals for their preservation.* Milwaukee, Wisconsin: Zoological Society of Milwaukee County.

Thornthwaite, C. W. & Mather, J. R. 1962. Average climatic water balance of the continents, Part 1, Africa. *Publications in Climatology*, **15** (2). Laboratory of Climatology, Centerton, New Jersey.

Tokura, H., Hara, F., Okada, M., Mekata, F. & Ohsawa, W. 1975. Thermoregulatory responses at various temperatures in some primates. In: *Contemporary Primatology* (Ed. By S. Kondo, M. Kawai & A. Ehara), pp. 171-176. Karger: Basel.

Tooby, J., & deVore, I. 1987. The reconstruction of hominid behavioural evolution through strategic modelling. In: The Evolution of Human Behaviour. Primate Models (Ed. by W. G. Kinzey), pp. 183-238. State University of New York Press, New York.

Tuhkanen, S. 1980. Climatic parameters and indices in plant geography. *Acta phytogeogr. suec.* **67**, 9-110.

Tutin, C. E. G., Fernandez, M., Rogers, E. M., Williamson, E. A. & McGrew, W. C. 1991. Foraging profiles of sympatric lowland gorillas and chimpanzees in the Lopé Reserve, Gabon. *Proc. R. Soc. Lond. B.*, **334**, 179-186.

Tutin, C. E. G., White, L. J. T., Williamson, E. A., Fernandez, M. & McPherson, G. 1994. List of plant species identified in the northern part of the Lopé Forest, Gabon. *Tropics*, **3**, 249-276.

Tutin, C.E.G., & Fernandez, M. 1992. Insect-eating by sympatric lowland gorillas (*Gorilla g. gorilla*) and chimpanzees (*Pan t. troglodytes*) in the Lopé Reserve, Gabon. *Am. J. Primatol.*, **28**, 29-40.

Tutin, C.E.G., & Fernandez, M. 1993. Composition of the diet of chimpanzees and comparisons with that of sympatric lowland gorillas in the Lopé Reserve, Gabon. *Am. J. Primatol.*, **30**, 195-211.

Tutin, C.E.G., McGrew, W.C., & Baldwin, P.J. 1983. Social organization of savanna-dwelling chimpanzees, *Pan troglodytes verus*, at Mt. Assirik, Senegal. *Primates*, **24**, 154-173.

Tuttle, R. H. 1981. Evolution of hominid bipedalism and prehensile capabilities. *Phil. Trans. R. Soc. Lond.* B., **292**, 89-94.

Uehara, S. 1982. Seasonal changes in the techniques employed by wild chimpanzees in the Mahale Mountains, Tanzania, to feed on termites. *Pseudocanthotermes spinger. Folia Primatol.*, **37**, 44-76.

Uehara, S. & Nishida, T. 1984. Body weights of chimpanzees (*Pan troglodytes schweinfurthii*) of the Mahale Mountains National Park, Tanzania. *Am. J. Phys. Anthropol.*, **72**, 315-321.

Vervaecke, H., & van Elsacker, L. 1992. Hybrids between common chimpanzees and pygmy chimpanzees in captivity. *Mammalia*, **56**, 667-669.

Vrba, E. S. 1985*a*. Environment and Evolution: Alternative causes of the temporal distribution of evolutionary events. *A. Afr. J. Sci.*, **81**, 229-236.

Vrba, E. S. 1985*b*. Ecological and adaptive changes associated with early hominid evolution. In: *Ancestors: The Hard Evidence* (Ed. by E. Delson), pp. 63-71. Alan R. Liss: New York.

Vrba, E. S. 1988. Late Pliocene climatic events and human evolution. In: *Evolutionary History of the "robust" australopithecines* (Ed. by F. E. Grine), pp. 345-376. New York: Aldine de Gruyer.

Vrba, E. S. 1992. Mammals as a key to evolutionary theory. *J. Mamm.*, **73**, 1-28.

Vrba, E. S. 1994. An hypothesis of heterochrony in response to climatic cooling and its relevence to early hominid evolution. In: *Integrative Paths to the Past - Paleoanthropological Advances in Honor of F. Clark Howell* (Ed. by R. S. Corruccini & R. L. Ciochon), pp. 345-376. New Jersey: Prentice Hall.

Vrba, E. S., Denton, G. H., Partridge, T. C. & Burckle, L. H. (Eds). 1995. *Paleoclimate and Evolution.* New Haven: Yale University Press.

Walker, A. C. 1981. Dietary hypotheses on human evolution. *Phil. Trans. R. Soc. Lond.* B., **292**, 47-64.

Walker, A., Leakey, R. E., Harris, J. M & Brown, F. H. 1986. 2.5Myr *Australopithecus boisei* from west of Lake Turkana, Kenya. *Nature*, **322**, 517-522.

Wallis, J. & Mattama, H. 1993. Social and environmental factors influencing sleep / wake patterns in wild chimpanzees (Abstract). *Am. J. Primatol.*, **30**, 354.

Walsh, R. P. D. 1981. The nature of climatic seasonality. In: *Seasonality Dimension to Rural Poverty* (Ed. by R. Chambers, R. Longhurst & A. Pacey), pp. 11-29.

Walter, H. 1979. *Vegetation of the Earth and Ecological Systems of the Geobiosphere.* New York: Springer.

Watanuki, Y. & Nakayama, Y. 1993. Age difference in activity pattern of Japanese monkeys: effects of temperature, snow and diet. *Primates*, **34**, 419-430.

Watts, D. P. 1988. Environmental influences on mountain gorilla time budgets. *Am. J. Phys. Anthropol.*, **15**, 195-211.

Watts, D. P. 1994. Agonistic relationships between female mountain gorillas (*Gorilla gorilla berengei*). *Behav. Ecol. Sociobiol.*, **34**, 347-358.

Wernstedt, F. L. 1972. *World Climatic Data.* Climatic Data Press.

Wesselman, H.B. 1995. Of mice and almost-men: regional paleoecology and human evolution in the Turkana Basin. In: *Paleoclimate and Evolution* (Ed. by E. S. Vrba, G. H. Denton, T. C. Partridge & L. H. Burckle), pp. 358-368. New Haven: Yale University Press.

Wheeler, P.E. 1984. The evolution of bipedality and loss of functional body hair in hominids. J. Hum. Evol., 13, 91-98.

Wheeler, P.E. 1991*a*. The thermoregulatory advantages of hominid bipedalism in open equatorial environments: The contribution of increased convective heat loss and cuaneous evaporative cooling. J. Hum. Evol., 21, 107-115.

Wheeler, P.E. 1991*b*. The influence of bipedalism on the energy and water budgets of early hominids. J. Hum. Evol., 21, 107-136.

Wheeler, P.E. 1992*a*. The influence of the loss of functional body hair on the energy and water budgets of early hominids. J. Hum. Evol., 23, 379-388.

Wheeler, P.E. 1992*b*. The thermoregulatory advantages of large body size for hominids foraging in savannah environments. J. Hum. Evol., 23, 351-362.

Wheeler, P.E. 1993. The influence of stature and body form on hominid energy and water budgets; a comparison of Australopithecus and early Homo physiques. J. Hum. Evol., 24, 13-28.

Wheeler, P. E. 1994*a*. The thermoregulatory advantages of heat storage and shade-seeking behaviour to hominids foraging in equatorial savannah environments. *J. Hum. Evol.*, **26**, 339-350.

Wheeler, P. E. 1994*b*. The foraging times of bipedal and quadrupedal hominds in open equatorial environments (a reply to Chaplin, Jablonski & Cable, 1994). *J. Hum. Evol.*, **27**, 511-517.

Wheeler, P. E. 1996. The environmental context of functional body hair loss in hominids (a reply to Amaral 1996). J. Hum. Evol., 30, 367-371.

White, F.J. 1986. Behavioural ecology of the pygmy chimpanzee. Ph.D. Thesis. State University of New York, Stony Brook.

White, F.J. 1988. Party composition and dynamics in *Pan paniscus*. *Int. J. Primatol.*, **9**, 179-193.

White, F. J. 1989. Ecological correlates of pygmy chimpanzee social structure. In: *Comparative Socioecology: The Behavioural Ecology of Humans and Other Mammals* (Ed. by V. Standen & R. A. Foley), pp. 154-164. Oxford: Blackwell Scientific Publications.

White, F.J. 1992*b*. Activity budgets, feeding-behaviour, and habitat use of pygmy chimpanzees at Lomako, Zaire. *Am. J. Primatol.*, **26**, 215-223.

White, F. J. 1994. Food sharing in wild pygmy chimpanzees, *Pan paniscus*. In: *Current Primatology Vol.* II, *Social Development, Learning and Behaviour* (Ed. by J. J. Roeder, B. Thiery, J. R. Anderson & N. Herrenschmidt), pp. 1-10. Strasbourg: Université Louis Pasteur.

White, F. J. & Chapman, C. A. 1994. Contrasting chimpanzees and pygmy chimpanzees: nearest neighbour distances and choices. *Folia Primatol.*, **63**, 181-191.

White, F. J. & Lanjouw, A. 1992. Feeding competition in Lomako pygmy chimpanzees: variation in social organisation with party size. In: *Topics in Primatology, Vol I., Human Origins* (Ed. by T. Nishida, W. C. McGrew, P. Marler, M. Pickford & F. B. M. de Waal), pp. 69-79. Tokyo: Tokyo University Press.

White, F.J., & Wrangham, R.W. 1988. Feeding competition and patch size in the chimpanzee species *Pan paniscus* and *Pan troglodytes*. *Behaviour*, **105**, 148-164.

White, T. D., Suwa, G., & Asfaw, B. 1994. Australopithecus ramidus, a new species of early hominid from Aramis, Ethiopia. *Nature*, **371**, 306-312.

White, T. D., Suwa, G., & Asfaw, B. 1995. Corringendum: Australopithecus ramidus, a new species of early hominid from Aramis, Ethiopia. *Nature*, **375**, 88.

White, T. D., Suwa, G., Hart, W. K., Walter, R., WoldeGabriel, G., De Heinzelin, J., Clark, J. D., Asfaw, B., & Vrba, E. 1993. New discoveries of Australopithecus at Maka in Ethiopia. *Nature*, **371**, 330-333.

Whitmore, T. C. 1975. *Tropical Rainforests of the Far East.* Clarendon Press: Oxford.

Whittaker, R. H. 1965. Dominance and diversity in land plant communities. *Science* **147**, 150-160.

Whittaker, R. H. 1970. *Communities and ecosystems.* New York: Macmillan.

Wilkinson, L. 1987. *SYSTAT: The System for Statistics.* Evantson: III. STSTAT.

Williamson, D. K. 1996. A model of chimpanzee socioecology. *Am. J. Phys. Anthorpol.*, **S22**, 255.

Wittenberger, J. F. 1980. Group size and polygamy in social mammals. *Am. Nat.*, **115**, 197-222.

Wolda, H. 1978. Seasonal fluctuation in rainfall, food and abundance of tropical insects. *J. Anim. Ecol.*, **47**, 369-381.

WoldgGabriel, G., White, T. D., Suwa, G., Renne, P., de Heinzelin, J., Hart, W. K., & Heiken, G. 1994. Ecological and temporal placement of early pliocene hominids at Aramis, Ethiopia. *Nature*, **371**, 330-333.

Wrangham, R.W. 1975. *Behavioural Ecology of Chimpanzees in Gombe National Park, Tanzania.* Ph.D. Thesis. University of Cambridge.

Wrangham, R. W. 1979. On the evolution of ape social systems. *Soc. Sci. Info.*, **18**, 335-368.

Wrangham, R. W. 1980. An ecological model of female bonded primate groups. *Behaviour*, **75**, 262-300.

Wrangham, R. W. 1982. Mutualism, kinship, and social evolution. In: *Current Problems in Sociobiology* (Ed. by R. W. Wrangham, D. I. Rubenstein, R. I. M. Dunbar, B. C. R. Bertam & T. H. Clutton-Brock), pp. 238-257. Cambridge: Cambridge University Press.

Wrangham, R. W. 1986. Ecology and social relationships in two species of chimpanzees. In: *Ecological Aspects of Social Evolution* (Ed. by D. I. Rubenstein & R. W. Wrangham), pp. 352-378. Princeton: Princeton University Press.

Wrangham, R. W. 1987. The significance of African apes for reconstructing human social evolution. In: *The Evolution of Human Behaviour: Primate Models.* (Ed. by W. G. Kinzey), pp. 51-71. State University of New York Press, New York.

Wrangham, R. W. & Smuts, B. B. 1980. Sex differences in the behavioural ecology of chimpanzees in Gombe National Park, Tanzania. *J. Reprod. Fert. (Suppl.).*, **28**, 13-31.

Wrangham, R. W., Clark, A. P. & Isabirye-Basuta, G. 1992. Female social relationships and social organization of Kibale forest chimpanzee. In: *Topics in Primatology, Vol I, Human Origins* (Ed. by T. Nishida, W. C. McGrew, P. Marler, M. Pickford & F. B. M. de Waal), pp. 67-79. Tokyo: Tokyo University Press.

Wrangham, R. W., Conklin, N. L., Chapman, C. A. & Hunt, K. D. 1991. The significance of fibrous foods for Kibale Forest chimpanzees. *Phil. Trans. R. Soc. Lond. B.*, **334**, 171-178.

Wrangham, R. W., Gittelman, J. L. & Chapman, C. A. 1993. Constraints on group size in primates and carnivores: population density and day-range as assays of exploitation competition. *Behav. Ecol. Sociobiol.*, **32**, 199-209.

Wrangham, R.W., Rogers, M.E., Isabiyre-Basuta, G. 1993. Ape food density in the ground layer in the Kibale Forest Uganda. *Afr. J. Ecol.*, **31**, 49-57.

Wrogemann, D. 1992. *Wild chimpanzees in Lopé: Census method and habitat use.* Ph.D. Thesis, University of Bremen, Germany.

Yamagiwa, J., Maurhashi, T., Yumoto, T. & Mwanza, N. 1996. Dietary and ranging overlap in sympatric gorillas and chimpanzees in Kahuzi-Biega National Park, Zaïre. In: *Great Ape Societies* (Ed. by. W. C. McGrew, L. F. Marchant & T. Nishida), pp. 82-100. Cambridge: Cambridge University Press.

Yumoto, T., Uamigiwa, J., Mwanze, N. & Maruhashi, T. 1994. List of plant species identified in Kahuzi-Biega National Park, Zaire. *Tropics*, **3**, 295-308.

Zihlman, A. L. 1984. Body build and tissue composition of *Pan paniscus* and *Pan troglodytes* with comparison to other hominids. In: *They Pygmy Chimpanzee* (Ed. by R. L. Susman), pp. 179-200. New York: Plenum.

Zihlman, A. 1996. Reconstructions reconsidered: chimpanzee models and human evolution. In: *Great Ape Societies* (Ed. by W. C. McGrew, L. F. Marchant & T. Nishida), pp. 293-304. London: Cambridge University Press.

Zihlman, A. L., Cronin, J. E., Cramer, D. L., & Sarich, V. M. 1978. Pygmy chimpanzee as a possible prototype for the common ancestor of humans, chimpanzees and gorillas. *Nature*, **275**, 744-746.

APPENDICES

APPENDIX I.

Tables of Spearman rank correlations of environmental variables from different climatic data sources. Significant correlations in bold and italics.

Table I.1. Unlogged climate data from Thornthwaite & Mather (1960).

	AE	D	DIV	MO100	MO50	P	PE	S	ST
D	*-.5161*								
	N(49)								
	P .000								
DIV	*-.5843*	*.7441*							
	N(49)	*N(189)*							
	P .000	*P .000*							
MO100	*-.8196*	*.7275*	*.7429*						
	N(49)	*N(189)*	*N(189)*						
	P .000	*P .000*	*P .000*						
MO50	*-.7121*	*.8187*	*.8520*	*.8870*					
	N(49)	*N(189)*	*N(189)*	*N(189)*					
	P .000	*P .000*	*P .000*	*P .000*					
P	*.8385*	*-.6625*	*-.5733*	*-.8902*	*-.8048*				
	N(49)	*N(189)*	*N(189)*	*N(189)*	*N(189)*				
	P .000	*P .000*	*P .000*	*P .000*	*P .000*				
PE	*.4664*	*.5114*	.1296	-.0206	.1001	.0171			
	N(49)	*N(189)*	N(189)	N(189)	N(189)	N(189)			
	P .001	*P .000*	P .075	P .778	P .171	P .815			
S	*.6738*	*-.6989*	*-.3892*	*-.6975*	*-.6403*	*.8680*	*-.2973*		
	N(49)	*N(189)*	*N(189)*	*N(189)*	*N(189)*	*N(189)*	*N(189)*		
	P .000	*P .000*	*P .000*	*P .000*	*P .000*	*P .000*	*P .000*		
ST	*.0000*	*-.4011*	*-.5730*	*-.7906*	*-.7133*	*.7518*	*2662*	*3508*	
	N(5)	*N(145)*	*N(145)*	*N(145)*	*N(145)*	*N(145)*	*(145)*	*(145)*	
	P .000	*P .000*	*P .000*	*P .000*	*P .000*	*P .000*	*P .001*	*P .000*	
Z	*.5566*	*-.6947*	*-.9668*	*-.7236*	*-.7917*	*.5394*	.1194	*3473*	*5946*
	N(49)	*N(189)*	*N(189)*	*N(189)*	*N(189)*	*N(189)*	N(189)	*N(189)*	*N(145)*
	P .000	*P .000*	*P .000*	*P .000*	*P .000*	*P .000*	P .102	*P .000*	*P .000*

Table I.2. Logged climated data from Thornthwaite & Mather (1960).

	LAE	LD	LDIV	LMO100	LMO50	LP	LPE	LS	LST
LD	*-.4985*								
	N(48)								
	P .000								
LDIV	*-.5843*	*.7439*							
	N(49)	*N(183)*							
	P .000	*P .000*							
LMO100	*-.8185*	*.7090*	*.7263*						
	N(48)	*N(181)*	*N(185)*						
	P .000	*P .000*	*P .000*						
LMO50	*-.7496*	*.7441*	*.8002*	*.8661*					
	N(43)	*N(165)*	*N(166)*	*N(166)*					
	P .000	*P .000*	*P .000*	*P .000*					
LP	*.8385*	*-.6580*	*-.5733*	*-.8885*	*-.7970*				
	N(49)	*N(183)*	*N(189)*	*N(185)*	*N(166)*				
	P .000	*P .000*	*P .000*	*P .000*	*P .000*				
LPE	*.4664*	*.4983*	.1296	-.0186	.0953	.0171			
	N(49)	*N(183)*	N(189)	N(185)	N(166)	N(189)			
	P .001	*P .000*	P .075	P .802	P .222	P .815			
LS	*.0494*	*-.3323*	-.1021	*-.3882*	*-.2254*	*.7471*	-.1474		
	(31)	*N(132)*	N(138)	*N(134)*	*N(115)*	*N(138)*	N(138)		
	P .792	*P .000*	P .233	*P .000*	*P .015*	*P .000*	P .084		
LST	*1.0000*	*-.4534*	*-.5730*	*-.7939*	*-.7279*	*.7518*	*.2662*	-.0145	
	N(5)	*N(140)*	*N(145)*	*N(142)*	*N(128)*	*N(145)*	*N(145)*	N(112)	
	P .000	*P .000*	*P .000*	*P .000*	*P .000*	*P .000*	*P .001*	P .880	
LZ	*.5566*	*-.6982*	*-.9668*	*-.7058*	*-.7310*	*.5394*	-.1194	.0503	*.5946*
	N(49)	*N(183)*	*N(189)*	*N(185)*	*N(166)*	*N(189)*	N(189)	N(138)	*N(145)*
	P .000	*P .000*	*P .000*	*P .000*	*P .000*	*P .000*	P .102	P .558	*P .000*

Key: (for logged data, variables are the same, but with suffix 'L' to denote natural log). **AE** = annual evapotranspiration; **D** = water deficit; **DIV** = rainfall diversity index; **MO100** = number of months with <100mm rainfall; **MO50** = number of months with <50mm rainfall; **P** = mean annual rainfall (mm); **PE** = potential evapotranspiration; **S** = water surplus; **Z** = Simpson's index of rainfall diversity.

Table I.3. Climate data from Le Houerou & Popov (1980) unlogged correlations.

	ANPET	P	P2T	PET5	T
P	*-.6111*				
	N(394)				
	P.000				
P2T	*-.6980*	*.8464*			
	N(394)	*N(395)*			
	P.000	*P.000*			
PET5	*-.6856*	*.8809*	*.9700*		
	N(394)	*N(395)*	*N(395)*		
	P.000	*P.000*	*P.000*		
T	*.7142*	*-.3061*	*-.4833*	*-.4306*	
	N(394)	*N(395)*	*N(395)*	*N(395)*	
	P.000	*P.000*	*P.000*	*P.000*	
PET35	*-.6988*	*.8564*	*.9956*	*.9746*	*-.4695*
	N(394)	*N(395)*	*N(395)*	*N(395)*	*N(395)*
	P.000	*P.000*	*P.000*	*P.000*	*P.000*

Table I.4. Le Houerou & Popov (1980). Logged correlations.

	ANPETL	P2TL	PET35L	PET5L	PL
P2TL	*-.6622*				
	N(369)				
	P.000				
PET35L	*-.6600*	*.9946*			
	N(368)	*N(369)*			
	P.000	*P.000*			
PET5L	**.00**	**.00**			
	N(0)	**N(0)**	**N(0)**		
	P.	**P.**	**P.**		
PL	*-.6111*	*.8168*	*.8280*	.	
	N(394)	*N(370)*	*N(369)*	*N(0)*	
	P.000	*P.000*	*P.000*	*P.*	
TL	*.7142*	*-.4677*	*-.4467*	*.00*	*-.3061*
	N(394)	*N(370)*	*N(369)*	*N(0)*	*N(395)*
	P.000	*P.000*	*P.000*	*P.*	*P.000*

Key: ANPET = annual potential evapotranspiration; **P2T** = number of months where rainfall (in mm) is greater than twice the mean annual temperature (°C); **PET35** = 0.35×potential evapotranspiration; **PET5** = 0.5×potential evapotranspiration; **P** = mean annual rainfall (mm); **T** = mean annual temperature (°C).

Table I.5. Unlogged data. Data from Wernstedt (1972).

	DIV	DRY	ELEV	LAT	LONG	MO100	MO50	P2T	P	T
DRY	*.6407*									
	N(90)									
	P.000									
ELEV	*-.2914*	-.1915								
	N(182)	N(79)								
	P.000	P.091								
LAT	*.4617*	*.3571*	.0249							
	N(212)	*N(90)*	N(183)							
	P.000	*P.001*	P.738							
LONG	-.0193	*.2324*	*.4438*	.1098						
	N(212)	*N(90)*	*N(183)*	N(214)						
	P.779	*P.028*	*P.000*	P.109						
MO100	*.4528*	*.8301*	.0738	*.4560*	*.2743*					
	N(201)	*N(90)*	N(169)	*N(198)*	*N(198)*					
	P.000	*P.000*	P.341	*P.000*	*P.000*					
MO50	*.7533*	*.8801*	-.0698	*.5699*	*.2450*	*.7944*				
	N(215)	*N(90)*	N(182)	*N(212)*	*N(212)*	*N(201)*				
	P.000	*P.000*	P.349	*P.000*	*P.000*	*P.000*				
P2T	*-.6552*	*-.9976*	.2038	*-.3665*	*-.2307*	*-.8306*	*-.8860*			
	N(90)	*N(90)*	N(79)	*N(90)*	*N(90)*	*N(90)*	*N(90)*			
	P.000	*P.000*	P.072	*P.000*	*P.029*	*P.000*	*P.000*			
P	*-.3891*	*-.7880*	*-.1727*	*-.4612*	*-.3649*	*-.8627*	*-.8228*	*.7791*		
	N(215)	*N(90)*	*N(182)*	*N(212)*	*N(212)*	*N(201)*	*N(215)*	*N(90)*		
	P.000	*P.000*	*P.020*	*P.000*	*P.000*	*P.000*	*P.000*	*P.000*		
T	.1880	.0048	*-.6429*	*-.3491*	*-.3175*	-.1832	.0281	-.0188	.1420	
	N(104)	N(81)	*N(95)*	*N(106)*	*N(106)*	N(104)	N(104)	N(81)	N(104)	
	P.056	P.966	*P.000*	*P.000*	*P.001*	P.063	P.777	P.868	P.151	
Z	*-.9300*	*-.5268*	*.3021*	*-.4576*	.0507	*-.3693*	*-.6724*	*.5408*	*.3313*	*-.2343*
	N(215)	*N(90)*	*N(182)*	*N(212)*	N(212)	*N(201)*	*N(215)*	*N(90)*	*N(215)*	*N(104)*
	P.000	*P.000*	*P.000*	*P.000*	P.463	*P.000*	*P.000*	*P.000*	*P.000*	*P.017*

Table I.6. Logged data. Data from Wernstedt (1972).

	DIVL	ELEVL	LATL	LONGL	MO100L	MO50L	P2TL	PL	TL
ELEVL	*-.2914*								
	N(182)								
	P.000								
LATL	*.4617*								
	N(212)	N(183)							
	P.000	P.738							
LONGL	-.0193	*.4438*	.0972						
	N(212)	*N(183)*	N(213)						
	P.779	*P.000*	P.157						
MO100L	*.4445*	.0738	*.4558*	*.2659*					
	N(200)	N(169)	*N(197)*	*N(197)*					
	P.000	P.341	*P.000*	*P.000*					
MO50L	*.7328*	-.0891	*.5696*	*.2787*	*.7783*				
	N(208)	N(177)	*N(205)*	*N(205)*	*N(194)*				
	P.000	P.238	*P.000*	*P.000*	*P.000*				
P2TL	*-.6472*	.1647	*-.3707*	*-.2202*	*-.8144*	*-.8486*			
	N(88)	N(77)	*N(88)*	*N(88)*	*N(87)*	*N(82)*			
	P.000	P.152	*P.000*	*P.039*	*P.000*	*P.000*			
PL	*-.3891*	*-.1727*	*-.4612*	*-.3649*	*-.8607*	*-.8155*	*.7636*		
	N(215)	*N(182)*	*N(212)*	*N(212)*	*N(200)*	*N(208)*	*N(88)*		
	P.000	*P.020*	*P.000*	*P.000*	*P.000*	*P.000*	*P.000*		
TL	.1880	*-.6429*	*-.3426*	*-.3087*	-.1762	.0264	.0433	.1420	
	N(104)	*N(95)*	*N(105)*	*N(105)*	N(103)	N(98)	N(79)	N(104)	
	P.056	*P.000*	*P.000*	*P.001*	P.075	P.796	P.705	P.151	
ZL	*-.9300*	*.3021*	*-.4576*	.0507	*-.3599*	*-.6600*	*.5398*	*.3313*	*-.2343*
	N(215)	*N(182)*	*N(212)*	N(212)	*N(200)*	*N(208)*	*N(88)*	*N(215)*	*N(104)*
	P.000	*P.000*	*P.000*	P.463	*P.000*	*P.000*	*P.000*	*P.000*	*P.017*

Key: DIV = rainfall diversity index; **ELEV** = altitude of weather station (m); **LONG** = longitude; **LAT** = lattitude; **MO100** = number of months with <100mm rainfall; **M050** = number of months with <50mm rainfall; **P2T** = number of months where rainfall (mm) is greater than twice the mean annual temperature (°C); **P** = mean annual rainfall; **T** = mean annual temperature; **Z** = Simpson's index of rainfall diversity.

Table 1.7. Spearman rank correlations for climate data from Southern and Central America. Data from Wernstedt (1972).

	DIV	MO50	P	P2T	T
MO50	*.8403*				
	N(117)				
	P.000				
P	*-.3659*	*-.6940*			
	N(117)	*N(117)*			
	P.000	*P.000*			
P2T	*-.8400*	*-.9700*	*.6349*		
	N(115)	*N(115)*	*N(115)*		
	P.000	*P.000*	*P.000*		
T	.0488	-.0840	*.3710*	.0034	
	N(102)	N(102)	*N(102)*	N(102)	
	P.626	P.401	*P.000*	P.973	
Z	*-.9156*	*-.7570*	*.3045*	*.7513*	-.1082
	N(117)	*N(117)*	*N(117)*	*N(115)*	N(102)
	P.000	*P.000*	*P.001*	*P.000*	P.279

Key: DIV = rainfall diversity index; **MO50** = number of months with <50mm rainfall; **P** = mean annual rainfall; **P** = mean annual rainfall; **P2T** = number of months where rainfall (mm) is greater than twice the mean annual temperature (°C); **T** = mean annual temperature (°C); **Z** = Simpson's index of rainfall diversity.

APPENDIX II

Part 1. Tables of correlations between behavioural and environmental variables.

Table II.1. Table of Spearman rank correlations (2-tailed) between behavioural data (see table 3.6) and climate data (study year sources, see tables 3.4 & 3.5)

	TMOMAX	TMOMIN	TMOX	RHUMAM	RHUMPM	RHUMX	P	MO50	MO100	P2T	Z	ALT
DRYF	.2515	-.1796	.0838	.4617	.3591	.3591	***-.6347***	.4910	.6025	-.5524	.2994	-.2994
	N(8)	N(8)	N(8)	N(5)	N(5)	N(5)	***N(8)***	N(8)	N(8)	N(8)	N(8)	N(8)
	P .548	*P* .670	*P* .844	*P* .434	*P* .553	*P* .553	***P .091***	*P* .217	*P* .114	*P* .156	*P* .471	*P* .471
FEED	-.1754	-.3439	-.3278	.4708	.5296	.5296-.	1625	-.1671	.2933	.2262	.3762	.1185
	N(12)	N(12)	N(13)	N(6)	N(6)	N(6)	N(13)	N(13)	N(12)	N(12)	N(13)	N(13)
	P .585	*P* .274	*P* .274	*P* .346	*P* .280	*P* .280	*P* .596	*P* .585	*P* .355	*P* .480	*P* .205	*P* .700
MOVE	.2794	-.0580	.1476	.4030	.2239	.2239	-.0510	.0363	.1150	-.2142	-.0845	.0841
	N(12)	N(12)	N(13)	N(6)	N(6)	N(6)	N(13)	N(13)	N(12)	N(12)	N(13)	N(13)
	P .379	*P* .858	*P* .630	*P* .428	*P* .670	*P* .670	*P* .868	*P* .906	*P* .722	*P* .504	*P* .784	*P* .785
N	***.7193***	***.5158***	***.6336***	.3531	.0000	.0000	-.2314	-.0613	.0459	***-.5195***	-.0415	-.2920
	N(12)	***N(12)***	***N(13)***	N(6)	N(6)	N(6)	N(13)	N(13)	N(12)	***N(12)***	N(13)	N(13)
	P .008	***P .086***	***P .020***	*P* .492	*P*1.000	*P*1.000	*P* .447	*P* .842	*P* .887	***P .083***	*P* .893	*P* .333
REST	.0667	.1860	.2424	-.5002	***-.7945***	***-.7945***	.1433	.2897	-.4417	-.1237	***-.4786***	.1543
	N(12)	N(12)	N(13)	N(6)	***N(6)***	***N(6)***	N(13)	N(13)	N(12)	N(12)	***N(13)***	N(13)
	P .837	*P* .563	*P* .425	*P* .312	***P .059***	***P .059***	*P* .641	*P* .337	*P* .151	*P* .702	***P .098***	*P* .615
SOCIAL	.0070	.0281	.0165	***-.7945***	-.6179	-.6179	***.5895***	-.2173	-.1307	.2862	-.1245	.0275
	N(12)	N(12)	N(13)	***N(6)***	N(6)	N(6)	***N(13)***	N(13)	N(12)	N(12)	N(13)	N(13)
	P .983	*P* .931	*P* .957	***P .059***	*P* .191	*P* .191	***P .034***	*P* .476	*P* .685	*P* .367	*P* .685	*P* .929

Key: (Environmental variables): **TMOMAX** = mean monthly maximum temperature (°C); **TMOMIN** = mean monthly minimum temperature (°C); **TMOX** = mean monthly temperature (°C); **RHUMAM** = mean relative humidity (a.m.); **RHUMPM** = mean relative humidity (p.m.); **RHUMX** = mean daily relative humidity (°C); **P** = mean annual rainfall (mm); **MO50** = number of months with <50mm rainfall; **M0100** = number of months with <100mm rainfall; **P2T** = number of months where rainfall (mm) is greater than twice the mean annual temperature (°C); **Z** = Simpson's index of rainfall diversity; **ALT** = altitude (m). **(Behavioural variables): DRYF** = dry season feeding time (%); **FEED** = feeding time (%); **MOVE** = moving time (%); **N** = group size; **REST** = resting time (%); **SOCIAL** = social time (%).

Table II.2. Spearman rank correlations (2-tailed) between baboon behavioural data and climate data (Climate data from table 3.7). Climate data from a mixture of long-term and short-term sources, emphasising proximity of weather records to baboon field sites (all values logged, significant correlations (<0.10) in bold and italic)

	FEED	MOVE	REST	SOCIAL	DRYFEED	N	DJL
P2T	.2262	-.2142	-.1237	.2862	-.5524	***-.5195***	-.5698
	N(12)	N(12)	N(12)	N(12)	N(8)	***N(12)***	-N(8)
	P .480	*P* .504	*P* .702	*P* .367	*P* .156	***P .083***	*P* .140
Z	.3939	-.1724	-.4298	-.0386	.1317	-.2424	-.1423
	N(13)	N(13)	N(13)	N(13)	N(8)	N(13)	N(9)
	P .183	*P* .573	*P* .143	*P* .900	*P* .756	*P* .425	*P* .715
MO100	.2523	.2994	-.2893	-.0246	***.7537***	.2708	.5052
	N(10)	N(10)	N(10)	N(10)	***N(6)***	N(10)	N(7)
	P .482	*P* .401	*P* .418	*P* .946	***P .084***	*P* .449	*P* .247
MO50	-.3616	.0710	***.5981***	-.0807	.2196	-.0640	.1423
	N(13)	N(13)	***N(13)***	N(13)	N(8)	N(13)	N(9)
	P .225	*P* .818	***P .031***	*P* .793	*P* .601	*P* .835	*P* .795
ALT	.1185	.0841	.1543	.0275	-.2994	-.2920	-.5774
	N(13)	N(13)	N(13)	N(13)	N(8)	N(13)	N(9)
	P .700	*P* .785	*P* .615	*P* .929	*P* .471	*P* .333	*P* .104
DIV	-.4105	.1599	.4316	.1509	-.1317	.2491	-.2755
	N(12)	N(12)	N(12)	N(12)	N(8)	N(12)	N(8)
	P .185	*P* .620	*P* .161	*P* .640	*P* .756	*P* .435	*P* .509
TMAX	.1754	.2794	.0667	.0070	.2515	***.7193***	.5607
	N(12)	N(12)	N(12)	N(12)	N(8)	***N(12)***	N(9)
	P .585	*P* .379	*P* .837	*P* .983	*P* .548	***P .008***	*P* .116
TMIN	-.3439	-.0580	.1860	.0281	-.1796	.5158	.4268
	N(12)	N(12)	N(12)	N(12)	N(8)	N(12)	N(12)
	P .274	*P* .858	*P* .563	*P* .931	*P* .670	*P* .086	*P* .252
TX	-.3278	.1476	.2424	.0165	.0838	***.6336***	.4603
	N(13)	N(13)	N(13)	N(13)	N(8)	***N(13)***	N(9)
	P .274	*P* .630	*P* .425	*P* .957	*P* .844	***P .020***	*P* .213
P	-.1625	-.0510	.1433	***.5895***	***-.6347***	-.2314	***-.7615***
	N(13)	N(13)	N(13)	***N(13)***	***N(8)***	N(13)	***N(9)***
	P .596	*P* .868	*P* .641	***P .034***	***P .091***	*P* .447	***P .017***

Key: (Environmental variables): P2T = number of months where rainfall (mm) is greater than twice the mean annual temperature (°C); **Z** = Simpson's index of rainfall diversity; **MO100** = number of months with <100mm rainfall; **MO50** = number of months with <50mm rainfall; **ALT** = altitude (m); **DIV** = rainfall diversity index; **TMAX** = mean maximum temperature (°C); **TMIN** = mean minimum temperature (°C); **TX** = mean annual temperature (°C). **(Behavioural variables): FEED** = feeding time (%); **MOVE** = moving time (%); **REST** = resting time (%); **SOCIAL** = social time (%); **DRYFEED** = dry season feeding time (%); **N** = group size; **DJL** = day journey length.

Table II.3. Spearman rank correlations (2-tailed) between baboon behavioural data and climate data (Climate data from table 3.3). Climate data from long-term sources, (Anon 1984). All values logged, significant correlations (<0.10) in bold and italic.

	FEED	MOVE	REST	SOCIAL	DRYFEED	N	DJL
P2T	.3737	-.0295	-.2810	.0562	-.1350	-.3344	-.1795
	N(13)	N(13)	N(13)	N(13)	N(8)	N(13)	N(9)
	P .208	P .924	P .352	P .855	P .750	P .264	P .644
Z	***.4876***	-.1034	***-.5455***	-.1212	.4192	-.1543	-.1088
	N(13)	N(13)	***N(13)***	N(13)	N(8)	N(13)	N(9)
	P .091	P .737	***P .054***	P .693	P .301	P .615	P .781
MO100	-.1251	.3558	-.0227	-.3411	***.7365***	.3184	.2623
	N(13)	N(13)	N(13)	N(13)	***N(8)***	N(13)	N(9)
	P .684	P .233	P .941	P .254	***P .037***	P .289	P .495
MO50	-.3584	.3617	.0931	-.1298	.5559	.4459	.5340
	N(13)	N(13)	N(13)	N(13)	N(8)	N(13)	N(9)
	P .229	P .225	P .762	P .673	P .152	P .127	P .139
ALT	.1129	.0897	.1763	.0771	-.2275	-.2975	-.5439
	N(13)	N(13)	N(13)	N(13)	N(8)	N(13)	N(9)
	P .713	P .771	P .564	P .802	P .588	P .324	P .130
DIV	-.3851	.1639	.4759	.0963	.0476	.1513	-.1925
	N(13)	N(13)	N(13)	N(13)	N(8)	N(13)	N(9)
	P .194	P .593	P .100	P .754	P .911	P .622	P .620
TABMAX	-.1129	-.1476	-.1543	.2149	-.0120	.1873	4268
	N(13)	N(13)	N(13)	N(13)	N(8)	N(13)	N(9)
	P .713	P .630	P .615	P .481	P .978	P .540	P .252
TABMIN	-.2006	-.3647	.5350	.2432	-.4928	-.1033	-.5429
	N(10)	N(10)	N(10)	N(10)	N(6)	N(10)	N(6)
	P .578	P .300	P .111	P .498	P .321	P .776	P .266
TDAMAX	-.2727	-.1338	.1763	.0826	-.1796	.4408	.3431
	N(13)	N(13)	N(13)	N(13)	N(8)	N(13)	N(9)
	P .367	P .663	P .564	P .788	P .670	P .132	P .366
TDAMIN	-.2452	.0483	.2645	.1928	-.0838	.4959	.1255
	N(13)	N(13)	N(13)	N(13)	N(8)	N(13)	N(9)
	P .419	P .876	P .383	P .528	P .844	P .085	P .748
TDAX	-.2617	-.0952	.1873	.1047	.0120	.4738	.3766
	N(13)	N(13)	N(13)	N(13)	N(8)	N(13)	N(9)
	P .388	P .757	P .540	P .734	P .978	P .102	P .318
TMOMAX	-.1846	-.0648	-.0331	.1708	.0838	.2975	.3598
	N(13)	N(13)	N(13)	N(13)	N(8)	N(13)	N(9)
	P .546	P .833	P .915	P .577	P .844	P .324	P .342
TMOMIN	-.2551	-.4465	.4692	.3144	-.5586	-.1959	-.4286
	N(11)	N(11)	N(11)	N(11)	N(7)	N(11)	N(7)
	P .449	P .169	P .145	P .346	P .192	P .564	P .337
TMOX	-.2372	-.1961	.1103	.2345	-.2036	.3255	.3866
	N(13)	N(13)	N(13)	N(13)	N(8)	N(13)	
	P .435	P .521	P .720	P .441	P .629	P .278	P .304
P	.0607	-.0843	.0469	***.4966***	-.5868	-.3586	***.5422***
	N(13)	N(13)	N(13)	***N(13)***	N(8)	N(13)	***N(9)***
	P .844	P .784	P .879	***P .084***	P .126	P .229	***P .056***
PDAYS	.0248	-.0428	.0000	-.0992	-.2994	.2479	.4603
	N(13)	N(13)	N(13)	N(13)	N(8)	N(13)	N(9)
	P .936	P .890	P1.000	P .747	P .471	P .414	P .213
RHUM	.0690	***-.5594***	.0690	-.2124	-.2275	-.3890	.2259
	N(13)	***N(13)***	N(13)	N(13)	N(8)	N(13)	N(9)
	P .823	***P .047***	P .823	P .486	P .588	P .189	P .559
RHUMAM	.0559	-.4140	.2905	.0447	-.1977	***-.5140***	-.2639
	N(13)	N(13)	N(13)	N(13)	N(8)	***N(13)***	N(9)
	P .856	P .160	P .336	P .885	P .639	***P .072***	P .493
RHUMPM	.1963	***-.6224***	-.0274	-.2968	-.1160	-.2237	.1566
	N(11)	***N(11)***	N(11)	N(11)	N(6)	N(11)	N(8)
	P .563	***P .041***	P .936	P .375	P .827	P .508	P .711

Key: (Environmental variables): P2T = number of months where rainfall (mm) is greater than twice the mean annual temperature (°C); **Z** = Simpson's index of rainfall diversity; **MO100** = number of months with <100mm rainfall; **MO50** = number of months with <50mm rainfall; **ALT** = altitude (m); **DIV** = rainfall diversity index; **TABMAX** = absolute mean maximum temperature (°C); **TABMIN** = absolute mean minimum temperature (°C); **TDAMAX** = mean daily maximum temperature (°C); **TDAMIN** = mean daily minimum temperature (°C); **TDAX** = mean daily temperature (°C); **TMOMAX** = mean monthly maximum temperature (°C); **TMOMIN** = mean monthly minimum temperature (°C); **TMOX** = mean monthly temperature (°C); **P** = mean annual rainfall; **PDAYS** = rainy days; **RHUM** = relative humidity; **RHUMAM** = relative humidity (a.m); **RHUMPM** = relative humidity (p.m). **(Behavioural variables):** see key to table II.2.

Table II.4. Spearman rank correlations between behavioural and environmental variables. significant (<0.10) correlations in bold and italics. Climate and behavioural data from Dunbar (1992*b*).

	DRYFEED	DJL	F	M	N	R	S
P	-.4303	***-.7217***	-.0440	-.4659	***-.5985***	2222	***.5149***
	N(10)	***N(14)***	N(14)	N(14)	***N(14)***	N(14)	***N(14)***
	P .214	***P .004***	P .881	P .093	***P .024***	P .445	***P .060***
T	-.3830	.2618	***-.5545***	.1024	***.4840***	***.4664***	.2310
	N(10)	N(14)	***N(14)***	N(14)	***N(14)***	***N(14)***	N(14)
	P .275	P .366	***P .040***	P .728	***P .079***	***P .093***	P .427
MO50	***.5951***	***.7166***	.0580	***.5118***	***.6362***	-.2590	***-.5559***
	N(10)	***N(14)***	N(14)	***N(14)***	***N(14)***	N(14)	***N(14)***
	P .070	***P .004***	P .844	***P .061***	***P .014***	P .371	***P .039***
Z	-.0125	.1406	***.5023***	-.3051	-.1429	***-.5760***	-.2143
	N(10)	N(14)	***N(14)***	N(14)	N(14)	***N(14)***	N(14)
	P .973	P .632	***P .067***	P .289	P .626	***P .031***	P .462

Table II. 5. Correlations among behavioural variables:

FEED	***.8333***				
	N(8)				
	P .010				
MOVE	.0000	-.4044			
	N(8)	N(13)			
	*P*1.000	*P* .171			
N	.0952	-.2857	***.6960***		
	N(8)	N(13)	***N(13)***		
	P .823	*P* .344	***P .008***		
REST	-.4286	***-.6319***	-.1541	-.2363	
	N(8)	***N(13)***	N(13)	N(13)	
	P .289	***P .021***	*P* .615	*P* .437	
SOCIAL	-.5714	-.3846	.0688	-.1648	.1429
	N(8)	N(13)	N(13)	N(13)	N(13)
	P .139	*P* .194	*P* .823	*P* .590	*P* .642
	DRYF	**FEED**	**MOVE**	**N**	**REST**

APPENDIX II

Part 2. QBASIC program for predicting baboon maximum ecologically tolerable group size: *Papio* baboons. Equations in this example program (in bold) from Dunbar (1996*b*) (see table 3.11).

```
10   REM PROGRAM "BABMOD.MXN"
20   REM SYSTEMS MODEL OF BABOON TIME BUDGETS
30   REM [NAME OF DATABASE EQUATIONS DERIVED FROM]
40   OPEN "OUTDAT.TEM" FOR OUTPUT AS #1
50   LPRINT TAB(20);"BABOON ACTIVITY BUDGETS MODEL"
60   LPRINT
70   LPRINT
80   LPRINT
160  LPRINT TAB (20); "Maximum Ecologically Tolerable Group
     Size"                                                      Print title
170  LPRINT
180  LPRINT
190  LPRINT
     TAB(5);"Rain(mm);";TAB(16);"0";TAB(23);"5";TAB(30);"10";T  Print table
     AB(37);"5";TAB(44);"20";TAB(52);"25";TAB(60);"30";TAB(68)  headings
     ;"35";TAB(75);"40"
200  LPRINT TAB(5);"-------------------------------------"
210  LPRINT
220  DIM JD(20,8)
230  DIM MAXN(20,8)
240  DIM FD(20,8)
250  DIM MD(20,8)
260  DIM RD(20,8)                                              set up arrays
270  DIM SD(20,8)
280  DIM HD(20,8)
310  FOR K=0 TO 14
320  LET P =100+(200*K)                                        rainfall integers
330  FOR I=0 TO 7
340  V = 11.4897 - .0078*P+.0000015*P*P                        temperature
350  IF V > 12 THEN V = 12                                     integers
360  IF V < 0 THEN V = .1                                      Ecological
370  IF V<.1 GOTO 380 ELSE 400                                 equation
380  V=.1
390  LET T = 0+(5*I)
420  LET PW=0/1000
430  WM=42.705-31.709*PW+20.078*PW*PW-0.408*T                  body weight
440  WF=20.513-7.086*PW+4.843*PW*PW-0.259*T                    equations
450  W=(WM+WF)/2
470  H = 1.0401-0.01224*V-0.0034*T                             tree cover
480  IF H<.1 GOTO 490 ELSE 510
490  H=.1
500  GOTO 530
510  IF H>.9167 GOTO 520 ESLE 530
520  H=.9167
530  LET N=5
540  LET N1=5
590  JL=1.3444+.7935*LOG(N)-.4733*LOG(P)                       day journey
600  J=EXP(JL)                                                 length equation
610  J=J*10
620  J=INT(J)
640  IF T=0 THEN T=.1
650  IF T<30 GOTO 660 ELSE 680
660  FL=6.866+4.077*LOG(H)-.7945*LOG(T)-.3896*LOG(V)+.1546*JL
```

```
670  F=(W^.404/3.1884)*EXP(FL)
680  IF F>85 GOTO 690 ELSE 700
690  IF N1=1 GOTO 900
700  ML=2.006+.1629*LOG(N)+.2189*LOG(V)
710  M=(2.5979/W^.333)*EXP(ML)
720  SL=-2.275+1.32*LOG(N)-.0445*LOG(N)*LOG(N)
730  S=EXP(SL)
750  RL=.97-7.9234*LOG(H)+.6009*LOG(V)
751  R=EXP(RL)
752  IF R<5 GOTO 755 ELSE 756
755  R=5
756  SUM=F+M+R+S
760  IF SUM>100 GOTO 800
780  N=N+1
790  GOTO 590
800  MAXN (K,I)=N-1
810  FD(K,I)=INT(F)
820  MD(K,I)=INT(M)
830  RD(K,I)=INT(R)
840  SD(K,I)=INT(S)
860  JD(K,I)=INT(J)
890  NEXT I
900  LPRINT TAB(4); P; TAB(10) ;"MaxN"; TAB(15); MAXN(K,0);
     TAB(21); MAXN(K,1); TAB(28); MAXN(K,2); TAB(35);
     MAXN(K,3); TAB(42); MAXN(K,4) ;TAB(50); MAXN(K,5);
     TAB(58); MAXN(K,6); TAB(66); MAXN(K,7); TAB(74);
     MAXN(K,8)
910 NEXT K
920 LPRINT
930 LPRINT TAB(5)"---------------------------------------"
940 END
```

day journey length equation moving time

social time (Dunbar 1991)

sum time budget

output arrays

print output

APPENDIX III.

Part 1. Periods of study and types of data recorded at chimpanzee and bonobo field sites.

Table III.1. Chimpanzee (*Pan troglodytes*) and bonobo (*Pan paniscus*) field sites and periods of study.

Site	Species studied	Location	Area (km^2)	Altitude (m)	Rainfall (period)	Vegetation	study period	methods
Bossou	*P.t.v.*	Guinea, Lola Prefecture	30	500-700	2000-3000	Primary and secondary forest, cultivated field, savanna	1976-1977, 1979-1980, 1982-1983, 1985-1986, 1987-present	foc. obs, ad lib, expt.
Gombe	*P.t.s.*	Tanzania, Kigoma region, 04°40'S 29°38'E	32	775-1500	1600	Evergreen riverine forest, deciduous dry forest, thicket, Miombo woodland, grassland, moorland	1960-present	nest follows, focal sampling.
Kahuzi-Biega	*P.t.s.*	Zaire, Province de Kivu, 02°S 28°E	6000	600-3308	1500-1900	Primary forest, secondary forest, swamp forest, bamboo, subalpine	1978-1979, 1987-present	group tracking, focal sampling, indirect evidence
Kibale	*P.t.s.*	Uganda, Kabarole District, 00° 34'N 30°22'E	560	1390-1625	1561-1859 (1984-1991)	Medium altitude moist evergreen forest, colonising forest-grassland, swamp communities	1978-1979, 1981(Ghiglieri), 1983-1985(Basuta), 1987-present	10-min focal samples during party observations
Lomako	*P.p.*	Zaire, Province de Equateur, 00°51'N 21°5'E	30 in 3500km^2 forest	390	1850 (1994)	primary evergreen and poly-specific forest, swamp forest	1974-91(intermittent) 1990-present	focal sampling, nest to nest, ad. lib.
Lopé	*P.t.t.*	Gabon, Ogooué-Ivindo, 00°10'S 11°35'E	50 in 5000km^2 forest	250-600	1168-1851 (1984-94)	Marantaceae forest closed canopy forest	1984-present	tracking, obs. when possible, DNA finger-printing

Table III.1. (Continued).

Site	Species studied	Location	Area (km^2)	Altitude (m)	Rainfall (period)	Vegetation	study period	methods
Mahale	*P.t.s.*	Tanzania, Kigoma Region, 06°07'S 29°44'E	11613	773-2515	1836 (1975-88)	Tropical semi-evergreen forest, Miombo woodland	1965-present	focal sampling
Nimba Mountains	*P.t.v.*	Ivory Coast, Yealé via Denané; Guinea, Nion via Lola; Liberia Lomako	50	400-1752	*	Primary forest	1986, 1993-present	All occurrence sampling, indirect evidence
Nouabalé-Ndoki	*P.t.t.*	Congo,Region de la Sangha, 2°10'-3°00'N 16°11'-17°00'E	4000	300-400	1430-1650 (1991-92)	Seasonal rain forest, semi-deciduous forest, evergreen forest, swamp forest, and swamp clearing	1989-92, 1994-present	Ad. lib sampling, indirect evidence
Taï Forest	*P.t.v.*	Ivory Coast, Sous Prefecture de Taï, 5°52'N 7°20'W	30 in 4260km^2 forest	160-245	1505-2150 (1988-93)	Evergreen moist rainforest	1976, 1979-present	Focal sampling, nest-to-nest
Ugalla	*P.t.s*	Tanzania, Kigoma-Mpanda Districts: main camp 5°19'S 30°37'E	2800	1100-1600	745-1280 (1973-88 at Uviza)	Grassy woodland, *Brachystegia-Julbernardia* miombo woodland	1985, 1988, 1992, 1993	Indirect evidence
Wamba	*P.p*	Zaire, Provincè Collectivite de Luo, Zone de Djolu, Sous-region de Tshuapa, 00°11'N 22°28'E	350	370-430	2000	Rainforest-derived mosaic of dry swamp, and secondary forest, cultivated fields	1974-81, 1983-91, 1994	Focal sampling, ad. lib.

APPENDIX III. Part 3.

QBASIC program for predicting chimpanzee maximum ecologically tolerable group size. Equations shown in bold, define ecological and time budget constraints.

```
10   REM PROGRAM "CHIMP.MXN"
20   REM SYSTEMS MODEL OF CHIMPANZEE TIME BUDGETS
30   REM [NAME OF DATABASE EQUATIONS DERIVED FROM]
40   REM OPEN "OUTDAT.TEM" FOR OUTPUT AS #1
50   LPRINT TAB(20);"CHIMPANZEE ACTIVITY BUDGETS MODEL"
60   PRINT
70   LPRINT
80   LPRINT
160  LPRINT TAB (20); "Maximum Ecologically Tolerable Group
     Size"                                                      Print title
170  LPRINT
180  LPRINT
190  LPRINT                                                     Print table
     TAB(5);"Rain(mm);";TAB(16);"0";TAB(23);"5";TAB(30);"10     headings
     ";TAB(37);"5";TAB(44);"20";TAB(52);"25";TAB(60);"30";T
     AB(68);"35";TAB(75);"40"
200  LPRINT TAB(5);"------------------------------------"
210  LPRINT
220  DIM JD(20,8)
230  DIM MAXN(20,8)
240  DIM FD(20,8)
250  DIM MD(20,8)
260  DIM RD(20,8)                                               set up arrays
270  DIM SD(20,8)
280  DIM HD(20,8)
290  DIM PRTD(20,8)
300  DIM DEND(20,8)
310  FOR K=0 TO 14
320  LET P =100+(200*K)                                         rainfall integers
330  FOR I=0 TO 8
340  LET T=0+(5*I)                                              temperature
350  REM V=7.9571-0.00302*P                                     integers
360  V = 8.1656-0.00253*P                                       Ecological
370  IF V<.1 GOTO 380 ELSE 400                                  equation
380  V=.1
390  GOTO 420
400  IF V>12 GOTO 410 ELSE 420
410  V=12
420  LET PW=0/1000
430  WM=42.705-31.709*PW+20.078*PW*PW-0.408*T                   body weight
440  WF=20.513-7.086*PW+4.843*PW*PW-0.259*T                     equations
450  W=(WM+WF)/2
460  REM H=0.4806+0.0407*T-0.00101*T*T
470  H = 1.0401-0.01224*V-0.0034*T                              tree cover
480  IF H<.1 GOTO 490 ELSE 510
490  H=.1
500  GOTO 530
510  IF H>.9167 GOTO 520 ESLE 530
520  H=.9167
530  LET N=5
540  LET N1=5
590  DENL=-18.925+.2624*LOG(N)+2.5338*LOG(P)                    density equation
600  DENS=EXP(DENL)
610  HRL=3.633-.8326*LOG(DENS)-9.3999E-02*(V)                   homerange
```

```
620  HR=EXP(HRL)                                                    equation
640  PRTL = -8.344+1.374*LOG(P)+.0418*LOG(V)-.0208*LOG(N)           party size
650  PRT=EXP(PRTL)                                                  equation
660  IF PRT<1 THEN PRT=1
670  IF PRT?N THEN PRT=N
680  JL=2.8792-.6349*HRL                                            day journey
690  J=EXP(JL)                                                      length equation
700  JS=J*10
710  JZ=INT(JZ)
720  IF T=0 THEN T=.1
730  UF T=0 THEN T=.1
750  FL=4.885-.6744*LOG(PRT)-.081*DENL+.65*3.12-.65*LOG(T)          feeding time
751  REM  Feeding equation first removes the                        equation
     thermoregulatory component using the slope 0.65 from
     baboons at the mean tempf ro the sites where feeding
     data derive (MEAN T=22.65°C, range 19.8-24.3)
752  REM  then incopriates and adjustment to inlude the
     thermoregulatory effects of temperature.
755  IF T<31 GOTO 780
756  TT=T-30
760  FL=FL+.65*LOG(TT)                                              feeding time
780  F=EXP(FL)
790  F=(W^.404/3.1844)*EXP(FL)                                      adjust for body
800  IF>.85 GOTO 819                                                body weight
810  IF N1=1 GOT0 1300
820  ML=2.9054+.02858*LOG(V)-.049*LOG(T)+.0458*LOG(DENS)            moving time
830  M=(2.5979/W^.333)*EXP(ML)                                      equation
840  M=EXP(ML)
860  SL=-2.275+1.32*LOG(N)-.0445*LOG(N)*LOG(N)                      social time
890  S=EXP(SL)                                                      equation
900  R=.97-7.9234*LOG(H)+.6009*LOG(V)                               resting time
920  R=EXP(RL)                                                      equation
940  IF R<5 GOTO 950 ELSE 970
950  R=5
960  REM assumes minimum R=5%, increasing proportional to
     C.
970  SUM=F+M+R+S                                                    sum timebudgets
980  IF SUM<90 GOTO 990 ELSE 1020
990  N=N+20
1000 N1=20
1100 IF N1=20 GOT 1100 ESLE 1140
1010 GOTO 590
1020 IF SUM<95 GOTO 1030 ELSE 1060
1030 N=N+5
1040 N1=5
1050 GOTO 590
1060 IF SUM<=100 GOTO 1070 ELSE 1100
1070 N=N+1
1080 N1=1
1090 GOTO 590
1100 IF N1=20 GOTO 1110 ELSE 1140                                   iterate maximum
1110 IF N=N-15                                                      ecologically
1120 N1=5                                                           tolerabe group
1130 GOTO 590                                                       size
1140 IF N1=5 GOTO 1150 ELSE 1180
1150 N=N-4
1160 N1=1
1170 GOTO 590
```

```
1180 MAXN(K,I)=N-1
1200 PRTD(K,I)=INT(PRT)
1210 DENS=DENS*10
1220 HD(K,I)=INT(HR)
1230 DEND(K,I)=INT(DENS/10)
1240 FD(K,I)=INT(F)
1250 MD(L,I)=INT(M)
1260 RD(K,I)=INT(R)
1270 SD(K,I)=INT(S)
1280 JD(K,I)=J/10
1290 IF MAXN(K,I)<0 THEN 1300 ELSE 1310
1300 MAXN(K,I)
1310 NEXT I
1320 LPRINT TAB(4); P; TAB(10) ;"MaxN"; TAB(15); MAXN(K,0);
     TAB(21); MAXN(K,1); TAB(28); MAXN(K,2); TAB(35);
     MAXN(K,3); TAB(42); MAXN(K,4) ;TAB(50); MAXN(K,5);
     TAB(58); MAXN(K,6); TAB(66); MAXN(K,7); TAB(74);
     MAXN(K,8).
1330 NEXT K
1340 LPRINT
1350 LPRINT TAB(5)"---------------------------------------"
1360 END
```

ouput arrays

print output in a table